Tesis doctoral

Invasiones biológicas en islas: dinámicas, impactos y gestión

Memoria presentada por Dña. Lucía Latorre Piñeiro para optar al grado de Doctora en Biología.

Santiago de Compostela, 8 de julio de 2013

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CERTIFICAN

Que la presente memoria con título "Invasiones biológicas en islas: dinámicas, impactos y gestión" elaborada por la licenciada en Biología Dña. Lucía Latorre Piñeiro, ha sido realizada bajo la dirección de D. Luis E. Santamaría Galdón y D. Asier Rodríguez Larrinaga y tutoría de D. Jesús Domínguez Conde, en el área de Zoología del Departamento de Zoología y Antropología Física de la Universidad de Santiago de Compostela. Considerándola concluida, autorizan su presentación al tribunal calificador para optar al Grado de Doctor en Biología.

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"Mientras no se reconozca que la Naturaleza no tiene fronteras políticas - que los animales migran cruzando amplios territorios, que los ríos pasan por muchos países, que los océanos bañan innumerables costas y que el aire lo respiramos todos- el deterioro ecológico de nuestro planeta continuará de manera inevitable."

Gerald Durrell & Lee Durrell.

"Si pretendemos entender qué es lo que ocurre en un equilibrio ecológico a nivel mundial, debemos examinar tanto el pasado como el futuro."

Charles Elton

"Como científicos que estudiamos y valoramos la naturaleza, debemos actuar en un punto medio entre aceptar pasivamente los cambios inevitables e intentar obsesivamente preservar el mundo como lo hemos conocido."

Mark A. Davis

A mis voluntarios de campo: Alicia, María, Xela, Fausto, Xabi, Laura, Fátima, Pablo, Bea y Borja.

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27 de septiembre de 2009.

Llego a la casa en la que me toca dormir esta temporada, que lle chaman "Vieira". Estoy algo cansada y a mis brazos y piernas casi no les queda espacio para un nuevo arañazo o picadura. Las Cíes de septiembre sostienen una hermosa y cruel población de mosquitos muy mal acostumbrados a la bonanza de sangre estival, mayormente de clase turista. Y de los toxos y silvas, nada hay que decir.

Estoy sola en la casa; no puedo hablar con nadie. Pienso. Y escribo. Huelo una mezcla de aceite al fuego, hierbas provenzales y mar.

Desde hace cuatro años duermo cerca del mar. Mis veinticinco años previos pertenecí a ese exótico cuarto de gallegos de interior; pero los traicioné para incluirme en la mayoría mariñeira, eso sí, medio atlántica-medio mediterránea. En este largo proceso me agoté. Por supuesto sufrí crisis (justas y necesarias) del tipo pero-qué-estoy-haciendo-y-para-qué-sirve-esto ?!. Estos cuatro años descuidé a mis amistades, olvidé mis aficiones y extrañé terriblemente la vida en pareja. Hablé con las plantas. Canté a grito pelado por los acantilados. Tuve alucinaciones. Discutí con fantasmas. Morí de calor y de frío. Me desesperé. Celebré San Xoán con sardiñas recién pescadas en Sálvora. Me desperté con los amaneceres más bonitos. Trabajé sin haber dormido. Escuché. Compartí. Discutí. Aprendí a no tener miedo de dormir sola en una isla solitaria. Aprendí a tolerar y entender a (casi) cualquiera.

Durante estos cuatro años hice lo que tenía que hacer. Lo que siempre estuvo ahí pero nunca tuvo un nombre o una imagen. Y eso ha sido el disfrutar la suerte más grande del mundo que es trabajar alimentando mi propia curiosidad.

Si estas palabras están ahora impresas, es que estos cuatro años de esfuerzo han merecido la pena.

6 de febrero de 2013

Hacer trabajo de campo en islas es de las experiencias más enriquecedoras que puede disfrutar una ecóloga principiante, sobre todo si eres de origen urbano.

En cuanto pones un pie en la isla, sientes una liberación casi violenta del

ritmo frenético de 'tierra firme' al que estás acostumbrada. La soledad diaria te va dando una claridad perceptiva única. Aparecen más y más 'momentos abismales' (gracias Miner), cercanos a lo lisérgico, en los que la angustia que te da su conocida brevedad no te deja encontrar papel y boli y, mucho menos, encontrar las palabras que expliquen ese *todo* que comprendes por segundos.

Con esa claridad puedes llegar a proyectar dinámicas ecológicas en las islas; y esta claridad no se daría si los medios isleños no fueran tan sencillos. Como dijo Mayr en 1967, cada isla es como si fuera un experimento en sí misma y nosotros tenemos la suerte de poder observar, analizar y dar con los resultados. Estos resultados obtenidos a esta escala (tú piensas, optimista) podrán ser extrapolables a redes mucho más extensas y procesos mucho más complejos. Pero estos momentos de iluminación resolutiva me temo que son en realidad, pequeños episodios, instantes de dominación ficticia de este sistema inabarcable en el que en realidad somos una más, insignificante, y del que no soportamos reconocer que somos meras observadoras.

Raramente estos momentos se dieron en mi caso delante de los crecientes montones de papers, descifrando modelos matemáticos, desarrollando textos y mucho menos dándole al *multitasking* que incluyó tareas de secretaria, técnico, coordinadora de proyectos, diplomática, profe, administrativa…etc.; lo cual es el pan nuestro de cada día para una becaria de ciencia en este nuestro país, especialmente en los primeros años.

Echando ahora la vista atrás y releyendo esos párrafos encapsulados en el tiempo, que suenan tan eufóricos como desesperados, veo esta experiencia únicamente como la mayor de las suertes, tanto para mi parte naturalista como para mi crecimiento personal.

Esta suerte que he tenido se complementó con el aporte de estas personas:

Giacomo Tavecchia, Alberto Velando, Ahimsa Campos Arcéiz "Maño", Fiona Tomás Nash: que involuntariamente definieron mi esquema del funcionamiento de este mundo paralelo que es la ciencia.

Luis y todos los voluntarios de la SEO, gracias. Todos los voluntarios del campo de traballo de las islas Cíes, gracias.

Todos y todas mis voluntarios/as, a los que va dedicada esta tesis: gracias, gracias, gracias. Sin vuestra ayuda estaría ahora mismo llorando en un

acantilado.

Farid, por tu apoyo en el inicio de esta carrera y haber compartido conmigo una buena parte de esta época tan importante. Vincent Rossi, hombre de agua.

Mis compis de gremio imedeos y amigos: Fiona, Raqueleta, Piter, Neus, Halpern, Fede, Aurore, María, Zeljka, Arantxa, Itzi, Amaya, Tomeu, Mar, Miquel, Iñigo, Anina, Johnna, Bea Carreja, y los que seguro me dejo. Sois lo mejor.

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A todo el personal de las islas:

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Sebas, mi hermano. Él ha creado la portada y el resto de dibujos. Gracias por compartir más allá.

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Luis Santamaría, cuya desbordante creatividad y contagiosa imaginación han sido las culpables de este mi trabajo.

Asier, sin palabras.

Todos los Latorre e tódolos Piñeiro.

Amanda.

Mi madre y mi hermana.

Mi padre, que me llevó a pasear a una lechuza y me contó historias de animales.

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RESUMEN

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Las islas son porciones de tierra rodeadas por mar. En lo humano, las islas son emplazamientos que han causado fascinación a aventureros/as, literatos/as y naturalistas. Esta fascinación se basa en la ventaja que supone la simplicidad y la singularidad de los sistemas isleños y sus dinámicas. Incluso Darwin y Wallace se vieron fuertemente influenciados por sus observaciones en las Galápagos y en el archipiélago indonesio para madurar sus teorías (Fernández-Palacios & Martín 2001), que probablemente no habrían desarrollado de haber permanecido siempre "en tierra firme".

Las islas conforman un 6% del total de superficie terrestre, y sus singularidades naturales son innumerables en lo que afecta a sus comunidades (alta proporción de organismos relictos, altas tasas de radiación adaptativa, alta proporción de organismos dioicos y de reproducción asexual) y a sus organismos (pérdida de poder de dispersión, tendencia hacia los extremos en tamaño, pérdida de capacidad de defensa; Fernández-Palacios & Martín 2001). Éstas son consecuencias de procesos biogeográficos que resultan, asimismo, en comunidades con una especial simplicidad: son ambientes homogéneos, disarmónicos (ecosistemas incompletos) y empobrecidos (menor número de especies que en territorios continentales equivalentes).

Sin embargo, simple no es sinónimo de fácilmente comprensible en el caso de las islas. Incluso en estos sistemas sencillos es muy difícil predecir las consecuencias de una alteración en su dinámica natural. Cada isla es un microcosmos de gran tamaño en el que cada impacto es especialmente dependiente del contexto; un experimento a gran escala cuya comunidad reacciona a pequeños cambios de manera altamente circunstancial (Mayr 1967). Por otro lado, a medida que aumenta la complejidad de estos sistemas y/o el impacto ejercido, más difícil resultan de entender y abarcar, como está ocurriendo en la actualidad con las invasiones por especies exóticas en los ecosistemas

insulares.

Las especies invasoras son especies introducidas por el hombre (de manera accidental o intencionada) en áreas ajenas a su rango de distribución natural, que ejercen algún tipo de daño sobre la biota nativa y/o se propagan muy rápidamente (Simberloff 2004; Davis 2009). Son uno de los componentes del cambio global (Chapin III *et al.* 2000) y conforman una enorme amenaza para la conservación de la biodiversidad a nivel mundial (Glowka *et al.* 1994; Wilcove *et al*. 1998; Clout 2001) y por lo tanto del acervo genético, funcionamiento, productividad y estabilidad de los ecosistemas (Chapin III *et al.* 2000, Balvanera *et al.* 2006). La incursión de especies exóticas en islas comenzó de la mano del inicio del tráfico marítimo hace aproximadamente 45.000 años (Balter 2007). Éste fue aumentando hasta la actualidad y con él, el ritmo de introducciones, y la extinción de especies causada por éstas (Diamond 1989). El creciente interés por las invasiones biológicas se materializó inicialmente en el influyente trabajo "The ecology of invasions by animals and plants" de C. Elton (1958). Aunque las invasiones ya se habían tratado como tal 200 años atrás (Chew 2006; Richardson & Pyšek 2007), éste fue un documento visionario y profético ya que gran parte versó, por primera vez, sobre la fragilidad y el riesgo del intercambio de especies, y predijo un ritmo irrefrenable de invasiones a nivel mundial. Efectivamente, la dispersión de especies ha aumentado exponencialmente desde los años 50 (Hulme 2011 y referencias ahí citadas) y con ellas, ha ido aumentando la preocupación social y científica, así como la literatura sobre el tema (Simberloff 2004; Ricciardi & MacIsaac 2008). Ésta inquietud no está injustificada, ya que las invasiones pueden afectar gravemente a la salud humana (McNeely 2005), a los ecosistema y su funcionamiento (Davis 2009) y, en consecuencia, a la economía. Los costes que suponen los tratamientos de exóticas son altísimos (Vilà *et al.* 2010). Pimentel *et al.* (2000) cuantificaron los costes del manejo de especies

exóticas en Estados Unidos en el año 1999 en 137 millones de dólares al año, lo que resultaría en cientos de millones de dólares anuales a nivel mundial (Davis 2009).

En la actualidad, el enfoque científico respecto a las invasiones es muy dispar (Simberloff 2004) y controvertido (Lodge & Schrader-Frechette 2003; Towns, Atkinson & Daugherty 2006), y abarca toda una gama de posicionamientos. Existen autores que ponen en duda la necesidad de una especialización desde la ecología o la macroecología como rama independiente (Blackburn 2004). Se dan también posturas derrotistas, autores que se resignan a las invasiones y las asumen como el resultado del devenir natural en la historia de la tierra (sugerido ya por Elton). Otros critican la "demonización" automatizada de las especies exóticas (Ewel & Putz, 2004) e incluso dudan de la gravedad real de sus impactos (Davis 2009). Sin embargo y por ahora, la tendencia más generalizada continúa siendo el temor a la homogeneización mundial impuesta por las plagas e invasiones (McKinney & Lockwood 1999; Rahel 2007).

Esta homogeneización es especialmente amenazante en las islas, por su falta de resiliencia ecológica. Es muy probable que los animales que llegan a islas (especialmente a remotas islas oceánicas) ocupen nichos ecológicos vacíos, ya que en muchas de ellas nunca han existido herbívoros y/o carnívoros de tamaño medio o grande, (Davis 2009 y citas ahí) lo que hará que, de llegar estos animales, las dinámicas tróficas cambien por completo. A esta mayor susceptibilidad de las islas ante las invasiones hay que añadir otro factor agravante, que es el alto grado de endemicidad de su biota (Blackburn *et al.* 2004; Cox & Lima 2006; Sax & Gaines 2008). Las especies invasoras suponen la segunda causa de pérdida de biodiversidad a nivel mundial (Chapin III *et al.* 2000) y la tasa de extinciones es mucho mayor en las islas que en los continentes (Brooke, Hilton & Martins 2007). Un 80 % de las extinciones conocidas desde la expansión

europea (aproximadamente desde el 1.500 de nuestra era hasta la actualidad) ha afectado a especies insulares; un 90 % si sólo se consideran aves, que han sido endémicas en su mayoría (Brooks 2000).

Por todas estas razones, las islas son espacios con una alta tasa de protección y las figuras que las amparan conllevan generalmente planes específicos de manejo de invasoras. Las acciones para controlar especies invasoras comenzaron hace 150 años (Elton 1958), promovidos por el departamento de Agricultura de los Estados Unidos, tras grandes pérdidas económicas por el tratamiento de plagas. Desde este momento hasta hoy, y siempre bajo el condicionante de la política y las prioridades de cada nación (Vander Zanden, Olden & Gratton 2006), la sociedad (asesorada por sus científicos) ha venido trabajando para el control de las especies invasoras. Para optimizar las metodologías de prevención y/o control de dichas especies en sus distintos estadíos, se ha definido el proceso invasor y sus distintas fases repetidamente (Davis 2009, Puth & Post 2005, Duncan, Blackburn & Sol 2003; Puth & Post 2005; Henderson, Dawson & Whittaker 2006; García-Berthou 2007; Davis 2009). Estas metodologías de intervención se circunscriben a tres tipos principales de acción de gestión: prevención, erradicación y control (Secretariat to the Convention on Biological Diversity 2001 en Hulme 2006).

En el caso de las islas, el evitar invasiones es un plan obviamente idealista. La predicción de la llegada de especies exóticas es muy complicada (Williamson & Fitter 1996) además de incierta (Worner & Gevrey 2006). La exclusión, erradicación o manejo efectivo de los impactos por invasoras que se debe asumir para asegurar la bioseguridad (Hulme 2011) son altamente costosos (Leung *et al.* 2002) y a menudo impracticables en continentes e islas de gran tamaño, ya que deben incluir un control constante con su correspondiente personal e instalaciones. Las erradicaciones son más efectivas en islas por su

reducido tamaño (en comparación con los continentes), su aislamiento y su menor necesidad de infraestructuras (Myers *et al.* 2000; Courchamp, Chapuis & Pascal 2003), aunque en la práctica no son mucho más comunes en islas que en continentes (Brooke, Hilton & Martins 2007).

Las erradicaciones exitosas van aumentando en número, y el tamaño de las islas donde se aplican es cada vez mayor (Simberloff 2002; Torr 2002; Nogales *et al.* 2004; Campbell & Donlan 2005; Martins *et al.* 2006), llegando incluso a los 1.000 km^2. Sin embargo, los planes de erradicación están a menudo rodeados de controversia (Blackburn *et al.* 2010) por sus costes desorbitados, por los fracasos tras aplicaciones inadecuadas (Banks 1999; Varnham *et al.* 2002), por sus efectos colaterales (considerados ya desde la época de Elton; Veitch & Clout 2002) y porque, dada su duración, su objetivo se logra en muchos casos demasiado tarde para evitar los impactos indeseados (Zavaleta, Hobbs & Mooney 2001).

Así, parece adecuada la consideración de planes de control alternativos a la erradicación, como la mitigación (Davis 2009), la contención (Hulme 2006) u otros (Myers *et al.* 2000 y citas ahí) que reduzcan la abundancia o la expansión de la especie invasora, así como los impactos sobre la biota nativa. La falta de consenso sobre la idoneidad del tratamiento de especies invasoras, tanto desde el plano teórico-científico como en la gestión práctica confirma la gran necesidad de profundidad en el estudio del proceso invasivo (Williamson 1999), no solo a escala general y teórica sino también desde el plano práctico y específico de cada caso. Cada plan de manejo debería incluir un estudio previo de la especie a tratar y el medio en el que se encuentra. Sólo con este tipo de estudios se pueden prever resultados realistas y positivos en términos de coste-resultado. Para ello es necesario una visón holística, que contemple la integridad ecológica (Hobbs *et al.* 2010), y enfocar la recuperación en la biodiversidad y su funcionalidad

(Ehrenfeld & Toth 1997; Zavaleta 2002). Y esto supone, a menudo, contemplar el conjunto de especies invasoras y sus interacciones simultáneamente, como partes del llamado "complejo de invasión" (Russell 2011).

La hipótesis de la naturalización**,** propuesta por Darwin (Davis 2009), considera que las especies no nativas que se establecen en un nuevo emplazamiento crean un nuevo equilibrio, una nueva red que conforma un "ecosistema adventicio" (Seastedt 2005) o "ecosistema novel" (Hobbs *et al.* 2006; Davis 2009), que tendrá más estabilidad cuanto más complejo sea (Robinson & Valentine 1979). Hoy en día es casi imposible encontrar una isla que contenga únicamente un animal invasor (e.g. Russell 2011, Canna Island; Bergstrom *et al.* 2009), por lo que aumenta la probabilidad de dar con ecosistemas noveles estables, conformados por redes de interacciones tróficas complejas que incluyan a las invasoras y a la biota nativa (Zavaleta 2002) y en los que se han desarrollado dinámicas ecológicas complejas (Russell 2011), como la *facilitación* (Simberloff & von Holle 1999; Bruno, Stachowicz & Bertness 2003) o la *hiperpredación* (Russell 2011). La probabilidad de encontrar este tipo de situaciones aumenta si hay varios depredadores presentes (Glen & Dickman 2005).

Por otro lado, a pesar de la singularidad de los ecosistemas isleños, podemos esperar que las consecuencias de sustraer una de las especies no difiera de las esperables en el continente (Zavaleta 2002), consecuencias tales como la *liberación de competidores* (Caut *et al.* 2007), la *liberación del mesodepredador* (Courchamp, Langlais & Sugihara 1999), *cascadas tróficas* (Croll *et al.* 2005) o *depredación intra-gremio* (Müller & Brodeur 2002). Sin estudios previos de las redes tróficas no resulta posible comprender estas dinámicas y predecir los resultados de sustraer elementos de (y por tanto, desensamblar) estas redes. Se han registrado cientos de ejemplos de resultados inesperados en respuesta al control o manejo de especies invasoras (Doak *et al.* 2008; Bergstrom *et al.* 2009),

sobre sistemas tanto simples como complejos (Courchamp, Langlais & Sugihara 1999; Courchamp, Langlais & Sugihara 2000; Zavaleta 2002; Courchamp, Chapuis & Pascal 2003; Hulme 2006; Caut, Angulo & Courchamp 2009). Para evitarlo, los estudios previos deben hacer hincapié en estas interacciones tróficas simples, pero sobre todo sobre las interacciones complejas (Vander Zanden, Olden & Gratton 2006) ya que cuanto más complejo es el ecosistema afectado, más probable es que haya un desensamblaje de la comunidad (Zavaleta 2009; Ruscoe *et al*. 2011) y más inesperados e impredecibles serán los resultados (Elmhagen & Rushton 2007). Aunque la realización de estudios previos del sistema puede permitir optimizar la planificación de las estrategias de actuación y el establecimiento de objetivos concretos, realistas y eficientes en términos de coste/resultado, es importante enfatizar la necesidad de incorporar programas de seguimiento que permitan la evaluación continua de la eficacia de estas acciones de control y el rediseño de las mismas (Zavaleta 2002; Vander Zanden, Olden & Gratton 2006; Heller & Zavaleta 2009; Hobbs *et al.* 2010).

Para estos estudios previos se han descrito varios protocolos generales y guías paso-a-paso (Parker *et al.* 1999; Zavaleta 2002). Sin embargo, hay mucho que mejorar en la definición y la capacidad predictiva de dichos trabajos, para aproximarse lo más posible al funcionamiento real del sistema invadido, utilizando la metodología más cuantitativa posible (Thomson 2005). Para entender cualquier dinámica ecológica compleja es necesario desgranar estas redes, conformadas tanto por relaciones sencillas como complejas. Las relaciones más sencillas entre invasoras y nativas son las que se establecen directamente (tanto antagonistas como mutualistas), y la manera más efectiva de evaluarlas es medir el impacto producido. Las relaciones complejas (que incluyen efectos indirectos mediados por terceras especies) pueden aparecer con mayor probabilidad al incrementar la cantidad de integrantes del complejo de invasión; aparte de una

mayor abundancia de impactos directos se incrementan también los impactos indirectos sobre la biota nativa (e. g. Fukami *et al.* 2006).

Los efectos directos de los animales invasores en islas se han estudiado abundantemente desde el inicio de la existencia de la biología de las invasiones como disciplina independiente. Estos estudios se han centrado sobre todo en especies ampliamente distribuidas y con graves impactos conocidos sobre las biotas nativas isleñas, como por ejemplo las diversas especies de ratas y su depredación sobre aves (Jones *et al.* 2008) o reptiles (Cree, Daugherty & Hay 1995), los agresivos episodios de herbivoría por parte del conejo europeo (Selkirk *et al.* 1983) o los impactos de gatos asilvestrados introducidos sobre gran cantidad de animales nativos (Medina *et al.* 2011). Mucho menos numerosos son los estudios de los efectos indirectos de los animales exóticos en islas, a pesar de que, en ocasiones, pueden resultar de igual relevancia, por ejemplo por disrupción de mutualismos planta-animal (Dohzono & Yokoyama 2010) o los efectos derivados de un incremento en el riesgo de depredación (Hayes *et al.* 2012). Muchos de estos efectos indirectos, también escasamente estudiados, se dan a través de terceras especies (St. Clair 2010), y pueden llevan a la aparición de dinámicas tróficas como la *hiperdepredación* (Roemer *et al.* 2001), y el surgimiento de mesodepredadores tras el control de superdepredadores (*liberación del mesodepredador*; Soule *et al.* 1988), o a la *facilitación* del establecimiento de especies exóticas nuevas a través de invasoras ya presentes (también conocido en inglés como *invasional meltdown*; Simberloff & Von Holle 1999). El estudio de este tipo de dinámicas es indispensable para la comprensión, identificación y cuantificación de todos los impactos causados por los grupos de especies invasoras.

El proceso de la *facilitación* ha sido bastante estudiado, especialmente relativo a herbívoros facilitando plantas invasoras (Relva & Veblen 1998; Nuñez,

Bailey & Schweitzer 2010) o entre herbívoros (Bakker, Olff & Gleishman 2009). Sin embargo, aún es escaso el conocimiento detallado acerca de la facilitación de una especie sobre otra y la relevancia específica como facilitadoras de las especies herbívoras respecto a otras (Nuñez, Bailey & Schweitzer 2010). La consideración de dinámicas más complejas como la *hiperdepredación* o la *liberación del mesodepredador* es más reciente. La relevancia de estas dinámicas en ambientes tan específicos como son las islas ha sido testado respecto a la *facilitación* (Simberloff 2006), pero son escasos los trabajos que traten acerca de la *hiperdepredación* o la *liberación del mesodepredador* en ambientes isleños (Morrison 2007; Medina & Nogales 2009).

En esta tesis he abordado el estudio del impacto de las especies invasoras y los complejos de invasión sobre la biota nativa insular. Para ello, he aumentado progresivamente la complejidad de mis sistemas de estudio. He evaluado así la relevancia relativa de los efectos directos y los efectos indirectos en sistemas de invasión sencillos y complejos, y he utilizado este conocimiento para intentar identificar las estrategias de gestión más adecuadas en términos de minimización de impactos sobre la biota nativa y prevención de potenciales efectos contra-intuitivos en complejos de invasión multiespecíficos (hiperpredación, liberación de mesodepredadores, liberación de competidores). Para ello he abordado el estudio de las interacciones comportamentales y tróficas que se conforman entre diferentes especies invasoras y con las diversas especies nativas, así como sus efectos directos e indirectos, mediante una combinación de observaciones empíricas y modelado.

Capítulo 1

Las aves marinas que anidan en islas suelen estar amenazadas por roedores invasores, como ratones y ratas, que atacan huevos, pollos e incluso los adultos de la colonia. Las erradicaciones de ratas suponen el método de protección óptimo, de ser factible. Sin embargo suelen ser objetivos impracticables en islas grandes, escarpadas o situadas cerca de la costa. En ese tipo de situaciones, la aplicación de planes de control y/o medidas de minimización de impacto puede representar una buena alternativa. En este trabajo, utilicé una combinación de experimentos de campo en una isla mediterránea con una población invasora de rata negra (*Rattus rattus*) con el objetivo de evaluar (1) el riesgo de depredación sobre los huevos de distintos tamaños de aves marinas y (2) el potencial de dos métodos distintos (disuasión electrónica *vs.* química) para reducir este impacto. Las ratas fueron capaces de consumir los huevos de todo el rango de tamaños ofrecidos (de 12 a 68 g de peso), pero la supervivencia de los huevos fue 13 veces mayor para los más grandes comparada con los más pequeños. La extrapolación sobre los tamaños de los huevos de las aves marinas presentes sugiere que la especie más pequeña (*Hydrobates pelagicus*) sufre el mayor riesgo de depredación, mientras que la especie mayor (*Larus michahellis*) podría sufrir un aumento de más del 60% de mortalidad en ausencia de vigilancia parental. La depredación sobre los nidos artificiales aumentó conforme avanzó el tiempo, lo que sugiere que las ratas aprenden a encontrar y explotar este recurso a lo largo de la época de cría. La aplicación de disuasivos químicos y electrónicos no redujo la proporción de nidos depredados. Sin embargo, la disuasión química (condicionamiento aversivo por cloruro de litio) redujo el incremento de la tasa de depredación, en comparación con el control y con la disuasión electrónica. Al final del período experimental, el efecto de la disuasión química se confirmó mediante un intercambio de tratamientos, que mostró que la protección adquirida

en los nidos experimentales permanece al menos 15 días tras el cese del tratamiento. Este estudio indica que es más probable que las especies pequeñas de aves marinas sufran tasas más severas de depredación por rata en los nidos y que el condicionamiento aversivo mediante químicos, (pero no los disuasivos electrónicos) pueden representar un método adecuado para proteger colonias cuando la erradicación o el control son impracticables o inefectivos.

Capítulo 2

Los herbívoros y granívoros representan unos de los moduladores más influyentes de la abundancia y la dinámica de población de las plantas. Sus efectos pueden ser, a su vez, modulados por factores bióticos o abióticos como la composición de comunidades, las características del hábitat o la heterogeneidad espacial. El estudio de los impactos de herbívoros y granívoros en las plantas debe, por tanto, considerar el efecto combinado de múltiples especies de herbívoros, los efectos de éstos sobre diferentes fases del ciclo vital de las plantas o el efecto de los gradientes medioambientales sobre estas interacciones. Sin embargo, los estudios de los efectos de múltiples especies de herbívoros sobre diferentes fases vitales de las plantas son aún escasos. En este trabajo, se ha estimado el efecto combinado de múltiples herbívoros exóticos (conejo europeo, *Oryctolagus cuniculus*; rata negra, *Rattus rattus*; y ratón casero, *Mus musculus*) sobre cuatro fases distintas del ciclo vital de una especie amenazada (*Medicago citrina*, Fabaceae). La mortalidad de semillas, plántulas y juveniles fue estimada en tres tipos de parcelas (abiertas, exclusión de rata y exclusión de rata y conejo) replicadas en cuatro sitios ($N = 3$ por sitio y tratamiento) en la isla de Cabrera (Islas Baleares, Mediterráneo occidental). El ramoneo sobre adultos reproductivos fue simulado en condiciones de jardín común (Jardín Botánico de Sóller, Mallorca) y se midió su efecto sobre el esfuerzo y el éxito reproductivo de las plantas control y tratadas. El conejo y la rata mostraron impactos complementarios sobre las

distintas fases de *M. citrina*. Éstos implicaron efectos independientes sobre las diferentes fases (consumo de semillas por rata, consumo de plántulas por conejo), lo que resultaría en un incremento multiplicativo en la mortalidad de la planta, y efectos simultáneos sobre la misma fase (ramoneo sobre juveniles). Además, el experimento de herbivoría simulada sobre adultos indicó que una eliminación moderada del follaje (25% de la biomasa inicial) es suficiente para causar un fuerte descenso en la producción de frutos por flor (de un 54 % a un 30 %); sin embargo el aumento en la intensidad de la eliminación de follaje no aumentó este efecto. Los resultados enfatizan la importancia de considerar los efectos simultáneos de varios herbívoros sobre distintas fases vitales de las plantas. Desde un punto de vista aplicado, los potenciales planes de reintroducción de *M. citrina* en Cabrera debe considerar medidas para, o bien controlar las poblaciones de ambos herbívoros exóticos, o bien mitigar sus impactos sobre fases tempranas de reclutamiento del ciclo de la planta (semillas, plántulas y juveniles).

Capítulo 3

Las invasiones biológicas suponen a menudo el establecimiento de múltiples especies invasoras, que forman los denominados complejos de invasión. Los complejos de invasión suponen amenazas adicionales sobre la biota nativa y pueden conllevar a efectos contraintuitivos tras acciones de gestión. En este trabajo, hemos evaluado la existencia y potencial interacción de dos efectos facilitativos entre cuatro especies establecidas en una isla continental: (1) la facilitación de pequeños (conejos) por grandes herbívoros (ciervos y caballos), e (2) hiperdepredación, denominación que recibe la competencia aparente entre presas nativas e invasoras (gaviotas y conejos) mediada por un depredador invasor (visón americano). Con este fin, combinamos observaciones de campo (demografía del conejo, abundancia del visón) con experimentos (exclusiones

de conejo y ungulados) y modelado demográfico. El resultado de las exclusiones de herbívoros, sumado al pico de abundancia de conejo tras un episodio de alta mortalidad de caballo, sugiere que la competencia por recursos predomina sobre la facilitación, por lo menos a corto plazo (dos años). El impacto de herbívoros invasores sobre especies nativas estuvo dominado por el efecto de los pequeños herbívoros (conejo). El visón fue capaz de recolonizar la isla tras tres campañas de control, principalmente migrando desde la costa cercana. La dependencia del visón de la presa invasora (conejo) ante la indisponibilidad de la presa nativa (gaviotas reproductoras) se tradujo en efectos de hiperdepredación. Las simulaciones indicaron que (1) en ausencia de programas de control, las gaviotas probablemente se extinguirán en un corto período de tiempo (una o dos décadas), y (2) la estrategia de control más efectiva es la combinación de control de conejo y visón. Sin embargo, dada la posibilidad del surgimiento de consecuencias inesperadas, se recomienda la reevaluación regular del plan de control elegido.

Capítulo 4

La introducción de varias especies invasoras conlleva a menudo el establecimiento de interacciones tróficas y de comportamiento, que llevan a consecuencias inesperadas tras acciones de control, como la liberación del mesodepredador, la hiperdepredación o la liberación del competidor. Hemos evaluado las interacciones entre cuatro mamíferos exóticos (dos depredadores, el visón americano y el gato asilvestrado; un mesodepredador, la rata negra; y un herbívoro, el conejo europeo) establecidos en dos islas continentales unidas (dos de las tres islas Cíes, NO España), así como su impacto sobre la flora nativa (armeria y camariña) y fauna (cormorán moñudo). Hemos combinado observaciones de campo (distribución espacial de todas las especies, abundancia y demografía de conejo y rata, dieta de gato y visón americano), experimentos de campo (exclusiones de herbivoría

y granivoría) y modelado demográfico para evaluar el impacto de mamíferos invasores y la idoneidad de distintas estrategias de control. Los resultados indican que estas especies invasoras han establecido interacciones que resultan en respuestas complejas a las acciones de manejo simuladas. En particular, ambos depredadores (visón americano y gato) depredan sobre ambas presas invasoras (conejo y rata) pero sólo uno de ellos (visón americano) tiene efectos relevantes sobre el cormorán. El modelado demográfico confirmó la potencial aparición de las tres respuestas contraintuitivas: (1) la liberación de la rata (como mesodepredador) tras el control del visón y/o gato, (2) la hiperdepredación de la presa nativa (cormorán) por el visón americano, mediada por la disponibilidad de presas exóticas (rata y conejo), y (3) la liberación del competidor entre el visón y el gato, mediado por sus presas comunes (rata y conejo). Sin embargo, dos de estos efectos sólo aparecen tras el control de múltiples especies invasoras (la liberación del mesodepredador tras controlar el visón y el gato, y la hiperdepredación tras controlar el visón y la rata). Más relevante es que sólo uno de estos efectos (la hiperdepredación) tuvo fuertes implicaciones para la conservación de las especies nativas (comprobado sobre el cormorán; los efectos por herbivoría no fueron incluidos en el modelo ya que se encontraron efectos significativos sobre las plantas nativas focales). Los resultados del modelo también indican que el control sobre el visón es la mejor estrategia sobre una sola especie, pero que los resultados sobre la población de cormorán mejorarían si las presas exóticas (sólo la rata o la rata y el conejo combinados) se incluyeran en las acciones de control al mismo tiempo. Los resultados del modelado ofrecen una evaluación preliminar de posibles acciones de gestión, las cuales deberían ser corroboradas con resultados reales de las acciones de control y rediseñadas acorde con ellas.

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Chapter 1

GENERAL INTRODUCTION

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Islands are portions of land surrounded by the sea. On their human dimension, islands have fascinated adventurers, writers and naturalists. This fascination is based on the advantage of the simplicity and singularity of island systems and their dynamics. Even Darwin and Wallace were strongly influenced by their observations in Galápagos and the Indonesian islands during the maturation of their theories (Fernández-Palacios & Martín 2001) which probably would not have happened had they stayed on *terra firma*.

Islands comprise 6% of the Earth's land. Their natural singularities are countless, in regard to their communities (high proportion of relict organisms, high rate of adaptive radiation, high proportion of dioecious and asexually reproducing species) and their organisms (loss of dispersal capacity, tendency to extreme sizes, loss of defense capability; Fernández-Palacios & Martín 2001). All these are consequences of biogeographic processes that also result in communities with a special simplicity; these environments are homogeneous, disharmonic (incomplete ecosystems) and impoverished (less species than in equivalent continental areas).

However, simple is not synonymous of easily understood in the case of islands. Even for these simple systems, it is very difficult to predict the consequences of any alteration in their natural dynamic. Each island is a large-sized microcosm, in which each impact is especially context-dependent; a large scale experiment whose community reacts to small changes in a highly circumstantial way (Mayr 1967). On the other hand, the higher the complexity of these systems and/or of the impacts they suffer, the more difficult to understand and control, as can currently be observed with biological invasions in island ecosystems.

Invasive species are species introduced by man (accidentally or intentionally) in areas outside of their natural distribution range, which exert a harmful effect on native biota and/or spread rapidly (Simberloff 2004; Davis 2009).

They are a component of the global change (Chapin III *et al*. 2000) and a great threat for the preservation of worldwide biodiversity (Glowka *et al.* 1994; Wilcove *et al*. 1998; Clout 2001) and hence, the genetic heritage, functioning, productivity and stability of ecosystems (Chapin III *et al.* 2000; Balvanera *et al.* 2006). The incursion of exotic species into islands around the world started with sea transport approximately 45,000 years ago (Balter 2007), and has been increasing to the present along with the rate of introductions and species extinction caused for them (Diamond 1989). The growing interest in biological invasions was initially materialized with the influential book "The ecology of invasions by animals and plants" by C. Elton (1958). Despite the fact that invasions had already been considered 200 years before (Chew 2006; Richardson & Pyšek 2007), this was a visionary and prophetic document, as it addressed for the first time the fragility and risk of species exchange, and predicted an uncontrollable rhythm of invasions. Species dispersal has in fact increased exponentially since the fifties (Hulme 2011 and citations therein) and with it, social and scientific concern on the issue and the specialized literature on the topic (Simberloff 2004; Ricciardi & MacIsaac 2008). This concern is justified, as invasions can seriously affect human health (McNeely 2005), ecosystems and their functioning (Davis 2009) and, hence, the economy. The management of exotic species involves very high monetary budgets (Vilà *et al.* 2010). Pimentel *et al.* (2000) quantified the costs of exotic species management in the U.S.A. in 1999 at 137 millions of dollars a year, an amount that would result in hundreds of millions of dollars on a global scale (Davis 2009).

The modern scientific approach to invasions is very diverse (Simberloff 2004), controversial (Lodge & Schrader-Frechette 2003; Towns, Atkinson & Daugherty 2006) and covers a wide range of opinions. Some authors doubt the necessity of a specialization from ecology or macroecology as an independent

branch (Blackburn 2004). There are also defeatist stances of authors who are resigned to assume invasions are a result of the natural progression of the Earth's history (already suggested by Elton), and even authors who criticize the automatic demonization of exotic species (Ewel & Putz 2004) and doubt the true gravity of their impacts (Davis 2009). However, the fear of world homogenization imposed by pests and invasions is still the most generalized trend (McKinney & Lockwood 1999; Rahel 2007).

This homogenization is even more threatening on islands, because of their lack of ecological resilience. Newly arrived animals will very likely occupy an empty ecological niche, as islands (especially remote oceanic ones) have typically not hosted middle or large-sized herbivores and/or carnivores (Davis 2009 and citations therein). Trophic dynamics will hence change completely with these new presences. Aside from the higher susceptibility of islands to biological invasions, another factor to consider is the high rate of endemicity of their biota (Blackburn *et al.* 2004; Cox & Lima 2006; Sax & Gaines 2008). Invasive species are the second cause of biodiversity loss worldwide (Chapin III *et al.* 2000) and the rate of extinctions is much higher on islands than on continents (Brooke, Hilton & Martins 2007). 80% of the known extinctions since the European expansion (approximately 1500 years ago until today) have affected island species; 90% considering only birds (most of them endemic; Brooks 2000).

For all of these reasons, islands worldwide hold a high rate of protection, and the preservation categories assigned to them normally entail specific plans for the management of invasive species. Plans for controlling invasive species started 150 years ago (Elton 1958), promoted by the Agriculture Department of the U.S.A., after large economic losses by pest treatments. Since that moment and always conditioned by politics and the priorities of each nation (Vander Zanden, Olden & Gratton 2006), society has been working for the control of invasions

with the cooperation of scientists. To optimize methodologies for prevention and/or control of these species in their varying statuses, the invasion process and its different phases has been repeatedly defined (Duncan, Blackburn & Sol 2003; Puth & Post 2005; Henderson, Dawson & Whittaker 2006; García-Berthou 2007; Davis 2009). The interventional methodologies hitherto proposed can be classified into three main types of management action: prevention, eradication and control (Secretariat to the Convention on Biological Diversity 2001 in Hulme 2006).

Regarding islands, prevention is a very idealistic plan, as prediction of the arrival of exotic species is highly complicated (Williamson & Fitter 1996) and uncertain (Worner & Gevrey 2006). Exclusion, eradication or effective avoidance of the impacts of invasive species that are assumed to ensure biosecurity (Hulme 2011) are very expensive (Leung *et al.* 2002) and often infeasible on continents and large-sized islands, as they involve constant control with the resulting needs for personnel and infrastructure. Eradication of invasive species is more effective on islands (as compared to mainland) due to their reduced areas, isolation and the need for simpler infrastructures (Myers *et al.* 2000; Courchamp, Chapuis & Pascal 2003), although in practice eradications are not much more common on islands than on continents (Brooke, Hilton & Martins 2007).

Successful eradications are increasingly abundant, as is the size of the affected islands (Simberloff 2002; Torr 2002; Nogales *et al.* 2004; Campbell & Donlan 2005; Martins *et al.* 2006), with success on islands as large as 1000 km^2. However, eradication plans are usually surrounded by controversy (Blackburn *et al.* 2010) given their disproportionate costs, the commonly reported failures after inappropriate applications (Banks 1999; Varnham *et al.* 2002), and their collateral effects (already considered in the times of Elton; Veitch & Clout 2002). Lastly, given their duration, objectives are often achieved too late to avoid the unwanted impacts (Zavaleta, Hobbs & Mooney 2001).

New control plans alternative to eradication seem to deserve consideration, such as mitigation (Davis 2009), contention (Hulme 2006) or others (Myers *et al.* 2000 and citations therein) that reduce the abundance and prevent the expansion of the invasive species, as well as limit impacts on native biota. The lack of consensus about the suitability of invasive species management, either on theoretical-scientific grounds or on the management practice, confirms the great need for continuing and deepening the study of the invasive process (Williamson 1999), not only in the general and theoretical scale but also from the practical point of view of each case. Each management plan should include a previous study of the species to be treated and the environment hosting it. Only with this kind of studies can we expect realistic and positive results with acceptable cost-efficiency ratios. To that end, we need a holistic vision which explicitly considers ecological integrity (Hobbs *et al.* 2010), and to focus the recovery on biodiversity and its functionality (Ehrenfeld & Toth 1997; Zavaleta 2002). This approach involves, commonly, the consideration of all the invasive species and their interactions simultaneously, as parts of the so-called integral invasion complex (Russell 2011).

The naturalization hypothesis, proposed by Darwin (Davis 2009) considers that non-native species that establish in a new location create a new equilibrium; a new web that generates an 'adventive ecosystem' (Seastedt 2005) or 'novel ecosystem' (Hobbs *et al.* 2006; Davis 2009), that will increase in stability with increasing complexity (Robinson & Valentine 1979). Nowadays it is almost impossible to find an island hosting a single invasive animal (e.g. Russell 2011, Canna Island; Bergstrom *et al.* 2009), making it more probable to find stable novel ecosystems, formed by webs of complex trophic interactions including both invasive and native biota (Zavaleta 2002) which have developed complex ecological dynamics (Russell 2011), such as *facilitation* (Simberloff & von Holle

1999; Bruno, Stachowicz & Bertness 2003) or *hyperpredation* (Russell 2011). The probability to find such new ecosystems increases when several predators are part of the invasion complex (Glen & Dickman 2005).

On the other hand, despite the singularity of island ecosystems, the consequences of removing one species should not be expected to differ from those of mainland systems (Zavaleta 2002), such as a *competence release* (Caut *et al.* 2007), a *mesopredator release* (Courchamp, Langlais & Sugihara 1999) a *trophic cascade* (Croll *et al.* 2005) or *intra-guild predation* (Müller & Brodeur 2002). It is not possible to understand these dynamics and predict the results of subtracting elements (and hence disassembling) these new webs without previous studies of their trophic relationships. Hundreds of examples have been recorded of unexpected results as a response to control or management of invasive species (Doak *et al.* 2008; Bergstrom *et al.* 2009), either on simple or complex systems (Courchamp, Langlais & Sugihara 1999; Courchamp, Langlais & Sugihara 2000; Zavaleta 2002; Courchamp, Chapuis & Pascal 2003; Hulme 2006; Caut, Angulo & Courchamp 2009). To avoid this, previous studies must emphasize the simple and complex interactions (Vander Zanden, Olden & Gratton 2006), given that the higher the complexity of the affected system, the more probable a disassembly of the community (Zavaleta 2009; Ruscoe *et al.* 2011) and the more unexpected and unpredictable the results (Elmhagen & Rushton 2007). Even though previous studies would optimize the planning of intervention strategies and the establishing of possible specific, realistic and efficient objectives, it is important to emphasize the need to incorporate monitoring programs that allow a continuous evaluation of the efficiency of these control actions and their redesign (Zavaleta 2002; Vander Zanden, Olden & Gratton 2006; Heller & Zavaleta 2009; Hobbs *et al.* 2010).

Several general protocols and step-by-step guides have been described for these previous studies (Parker *et al.* 1999; Zavaleta 2002). Nevertheless,

there is still a lot of work to do in regard to the definition and predictive capacity of these studies, in order to achieve the most realistic and quantitatively precise approximation to the real functioning of the invaded system (Thomson 2005). In order to understand any complex ecological dynamic, it is necessary to disentangle these webs, formed by simple as well as complex relationships. The simplest of these links between invasive and native species are those established directly (mutualistic or antagonistic) and their most effective evaluation is the measurement of the produced impact. Complex relationships (which include indirect effects mediated by third species) are more likely to appear with an increased number of species of the invasion complex; aside from the direct impacts, indirect impacts appear on the native biota (e. g. Fukami *et al.* 2006).

Direct effects of invasive animals have been widely studied since the early works on biological invasions. These works dealt especially with widespread species, which cause harmful impacts on island native biotas, as for example the different species of rats and their predation on birds (Jones *et al.* 2008) or reptiles (Cree, Daugherty & Hay 1995), aggressive episodes of herbivory by European rabbit (Selkirk *et al.* 1983) or the impacts of introduced feral cats which predate on many native species (Medina *et al.* 2011). Few are the studies about indirect effects of exotic animals on islands, even though they may hold the same relevance; e.g. plant-animal mutualism disruptions (Dohzono & Yokoyama 2010) or sub-lethal indirect effects resulting in an increase of predation risk (Hayes *et al.* 2012). Many of these indirect effects, which have also been poorly studied, arise through intervening third species (St. Clair 2011) and can lead to the appearance of trophic dynamics as *hyperpredation* (Roemer *et al.* 2001) and the arising of mesopredators after the control of superpredators (*mesopredator release*; Soule *et al.* 1988), or the *facilitation* of the establishment of new exotic species by already present invasives (also known as *invasional meltdown*; Simberloff &

Von Holle 1999). The study of these kinds of dynamics is indispensable for the understanding, identification and quantification of all the impacts caused by pools of invasive species. The process of facilitation has been fairly studied, especially concerning herbivores facilitating invasive plants (Relva & Veblen 1998; Nuñez, Bailey & Schweitzer 2010) or between herbivores (Bakker, Olff & Gleishman 2009). Nevertheless, more detailed knowledge about the *facilitation* of one exotic species on another and how important exotic herbivores are to other species is still lacking (Nuñez, Bailey & Schweitzer 2010). The consideration of more complex dynamics as *hyperpredation* or *mesopredator release* is more recent. The relevance of these dynamics in such specific environments as invaded islands has been documented in regard to *facilitation* (Simberloff 2006), but few works exist about *hyperpredation* and *mesopredator release* (Morrison 2007; Medina & Nogales 2009).

The first studies that consider invasion complexes integrally and identify both their direct and indirect effects are relatively recent. Still, they are progressively increasing their complexity and approaching a full quantitative description of the system, resulting in more precise predictions and simulations. **In this dissertation I assessed the study of the impact of invasive species and invasion complexes on island native biotas. I tried to do an exercise with a progressive increase in the complexity of the study of biological invasions in island ecosystems**. I evaluated the relative relevance of direct and indirect effects in simple and complex invasive systems, and used this knowledge to identify the most suitable management strategies in terms of minimizing the impacts on native biota and prevention of potential counterintuitive effects on multispecific invasion complex (hiperpredation, mesopredator release and competitor release). For this purpose I addressed the study of the behavioural and trophic interactions conformed among the invasive species and with the

native biota, as well as the direct and indirect effects, throughout a combination of empiric observations and modelling.

Outline of the thesis

In the first part of the dissertation (chapters 1 and 2) I studied the direct impacts of two invasive herbivores (black rat and European rabbit) in two Mediterranean island ecosystems. In the second part (chapters 3 and 4), I studied both impacts and the dynamics of two invasion complexes present in a coastal, Atlantic archipelago and composed by, respectively, three herbivores and a predator (feral horse, red deer, European rabbit and American mink, on Sálvora Island) and one herbivore, one mesopredator and two top predators (European rabbit, black rat, feral cat and American mink, on Cíes Islands).

In **chapter 1** I studied the direct impact of black rat (*Rattus rattus*) on the seabirds of Sa Dragonera Natural Park (Balearic Islands). I focused on the effect of egg size on predation by rats, and then I compared the efficiency of two alternative methods for the minimization of this impact. In **chapter 2** I analyzed the impact of two invasive herbivore species (*R. rattus* and *Oryctolagus cuniculus*) on four different phases of the recruitment cycle of a eastern Mediterranean endemism (the shrub *Medicago citrina*) in Cabrera Archipelago National Park. **Chapters 3** and **4** address the trophic and behavioural interactions within two different invasion complexes established at the Atlantic Islands of Galicia National Park, identify their impact on native biota, and used this information to evaluate different management strategies. In **chapter 3 I** studied the multiple interactions among the four-species invasion complex of Cíes Islands and related them to the impacts on native biota (native plants and seabirds) and the responses to management actions - paying particular attention to the potential impact of herbivore facilitation and hyperpredation upon them. For this purpose, I i) measured the abundance and demography of the invasive prey (rabbit) and predator (mink), ii) studied

the impact of large (horse and deer) and small (rabbit) invasive herbivores on native vegetation, and iv) used demographic modeling to simulate the responses of invasive rabbit and mink to different management strategies, to evaluate the importance of hyperpredation effects, and their potential impact on native prey of conservation interest (yellow-legged gull). In **chapter 4** I studied the multiple interactions among the four-species invasion complex of Cíes Islands and related them to the impacts on native biota and the responses to management actions. For this purpose, I i) measured the distribution and abundance of the four invasive species, ii) studied the diet of both top predators, including native and invasive prey, iii) estimated the direct effects of herbivores and granivores on native plants, and iv) simulated the demographic responses on the invasion complex to different management strategies, including the triggering of counterintuitive effects (mesopredator release, competitor release and/or hyperpredation), and their impact on native prey of conservation interest (European shag).

The work presented in this dissertation aimed at providing useful advice for management practices, making the results as applicable as possible. Hence, I have provided specific recommendations (e.g. on impact mitigation and control plans for invasive species) for conservation practitioners and decision makers. This is especially so in the case of the last two chapters where, based on the gathered data, I have developed demographic models and used them to simulate different management scenarios with the aim of assessing their efficiency.

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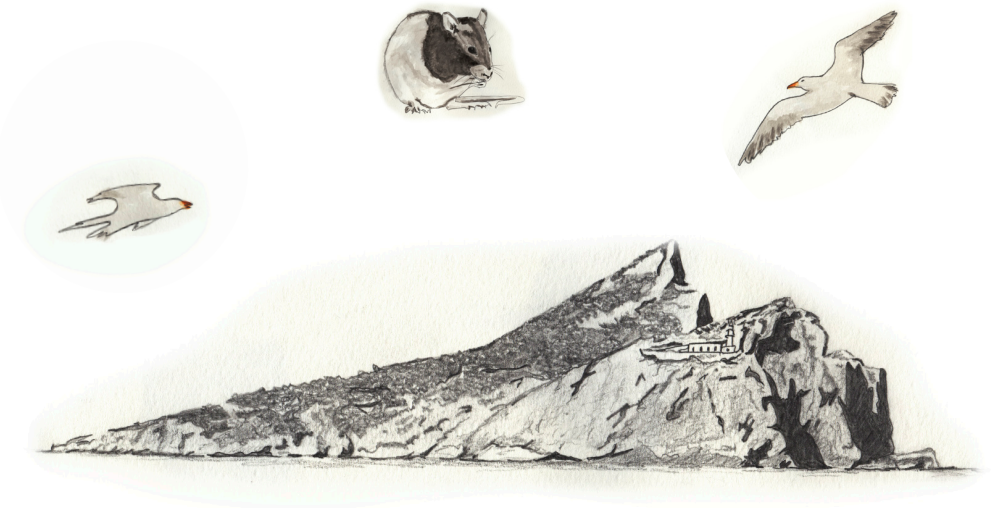
Chapter 2

Rats and seabirds: effects of egg size on predation risk and the potential of conditioned taste aversion as a mitigation method

Ratas y aves marinas: efectos del tamaño de huevo sobre el riesgo de depredación y el potencial del condicionamiento de aversión al sabor como método de mitigación



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2.1. Introduction

Biological invasions represent one of the global drivers of biodiversity loss (Vitousek *et al*. 1997; Ricciardi 2007). They often alter ecosystem structure and functioning, and their effects feed back to other elements of global change (Dukes *&* Mooney 1999). Islands are particularly prone to host species introductions (e.g. 80% of documented bird and mammal introductions took place on islands; Ebenhard 1988), which usually cause more intense impacts than on mainland ecosystems (Courchamp, Chapuis & Pascal 2003; but see Vilà *et al*. 2011 for plant invaders) owing to the rarity and evolutionary singularity of island biotas (often evolved without natural enemies and therefore lacking defensive traits against them; Bowen *&* van Vuren 1997; Blackburn *et al*. 2004). Moreover, because insular biotas tend to be less diverse than continental ones, they offer weaker resistance to biological invasions and more sensitivity to their effects (Loope *&* Mueller- Dombois 1989; Simberloff 2000), which often include cascades of native-species extinctions (Bergstrom *et al*. 2009; St. Clair 2011).

Islands are key habitats for nesting seabirds (Mayr 1965), largely because the absence or scarcity of terrestrial predators enhances reproductive success. The consequence of an evolutionary history free of predators at breeding colonies is however, that seabirds often lack defensive mechanisms against them (e.g. inaccessible nests, early independence of chicks), making them more prone to severe impacts from biological invasions by predatory mammals (Atkinson 1985; Courchamp, Chapuis & Pascal 2003; Ruffino 2009). Around 60% of the seabird species cited in the IUCN red list are under some level of risk by invasive animals (mainly mammals; Redstone Strategy Group 2008), most often through their effect on breeding colonies (Blackburn *et al*. 2004; Hilton *&* Cuthbert 2010). Amongst such predators, rats (particularly black rats; *Rattus rattus*) are considered to be

a direct cause of the vulnerable status of at least 75 island-nesting species of seabirds (Jones *et al*. 2008).

At present, rats occupy 82% of islands worldwide; most of them outside of their native ranges (Atkinson 1985). They are responsible for the decline and eventual elimination of many native animal species (Bertram & Nagorsen 1995; Towns 1996; Robinet, Craig & Chardonnet 1998; Thorsen *et al*. 2000; Salvande *et al*. 2006), through both direct (e.g. predation as in Brown *et al*. 1998; or, inter-specific competition; Brosset 1963) or indirect (Towns *et al*. 2009) effects. In particular, the decline of seabird populations in islands is often triggered by rat invasions (Atkinson 1985; Jones *et al*. 2008). In such cases, rat eradication programs (most often based on the application of poisonous bait; Howald *et al*. 2007) are sometimes sufficient to foster the recovery of seabird populations (Imber, Harrison & Harrison 2000; Amaral *et al*. 2010; Towns & Broome 2011). However, eradications are not always feasible (e.g. in large islands or those with rugged topography); they are often controversial (Towns, Atkinson & Daugherty 2006), owing to their high economic costs and the environmental risks involved (Myers *et al*. 2000); and they may be followed by re-colonization, if controls against the introduction of new individuals are not feasible or enforceable (Russell, Towns & Clout 2008). In such cases, alternative control techniques may include population-control programs (repeated reductions of rat abundance at particularly relevant or sensitive sites; Myers *et al*. 2000, Igual *et al*. 2006) or measures aimed at mitigating the rats' most relevant impacts. Given that such measures are specifically tailored to minimize the impacts of rat presence, a detailed understanding of such impacts is a pre-requisite for their design and cost-effective application. Unfortunately, knowledge of the processes underlying the harmful impacts of invasive rats on island-nesting seabirds is still fairly limited (Martin, Thibault & Bretagnolle 2000; Towns, Atkinson & Daugherty 2006; Russell, Towns & Clout 2008).

During the last decades, several authors have searched for the specific characteristics that make certain seabird species more sensitive to rat predation. Atkinson (1985) and Imber (1976) indicated that species with burrow or cavity nesting, as well as those included in the *Hydrobatidae* and *Alcidae*, were amongst the most affected. This hypothesis has been confirmed by a recent review (Jones *et al*. 2008) but the mechanism by which these species are particularly affected by rats, as compared to ground nesting species and/or those belonging to other families, remains unclear. Suggestions include the effect of nesting "microhabitat" (i.e. the birds' fossorial habits, which facilitate rats' access to the nests, and nocturnal activity patterns, which decrease nest defense when rats are also active; Jones *et al*. 2008) and/or nesting ecology (lack of active anti-predator defenses in burrow/cavity nesters, as compared to ground nesters; Lack 1968 in Jones *et al*. 2008; Hansell 2000; Wesolowski & Tomialojc 2005). Another characteristic that has received less attention, but tends to differentiate burrow/cavity nesters from ground nesters, is their smaller size (Jones *et al*. 2008). Smaller seabirds have been shown to be more sensitive to rat invasions (Martin, Thibault & Bretagnolle 2000), and a review by Jones *et al.* (2008) acknowledges that, owing to the confounding effects of size, family and nesting strategy, the relative effects of these factors remains unresolved.

Nest predation by rats may affect seabird eggs, chicks and adults. Eggs represent a particularly sensitive stage (since they fully depend on brooding adults for protection, apart from their intrinsic protection features as thickness or size). Because large eggs are more difficult to manipulate and tend to have thicker eggshells, it has been suggested that egg size may confer resistance against rat predation (Atkinson 1985). Evidence to date is scarce and controversial. On one hand, Jones *et al*. (2008) could not confirm this hypothesis, although the available data were too scarce for a robust conclusion. On the other hand, field

and laboratory experiments with hen eggs offered to black rats (Prieto *et al*. 2003), Japanese quail and zebra finch eggs offered to white-footed mice (DeGraaf & Maier 1996) and chipmunks (Haskell 1995) and Japanese quail and clay eggs offered to white-footed mice and chipmunks (Goodner, Jacobson & Goodner 1998) suggest that jaw-gape limitations and/or strong eggshells may constrain the ability of small rodents to predate on larger eggs (although behavioral naivety may also contribute to the observed responses; Haskell 1995; Prieto *et al*. 2003).

We tested this hypothesis by means of a field experiment, in which artificial nests containing eggs of four different sizes were subjected to predation by black rats at Sa Dragonera Islet (Mallorca Island), which hosts breeding colonies of several seabird species of contrasting body and egg sizes. In addition, we assessed the effectiveness of two non-invasive methods aimed at reducing egg predation in seabird colonies: (1) Induction of egg deterrence by conditioned taste aversion (CTA; Garcia, Kimeldorf & Koelling 1955; Garcia, Hankins & Rusiniak 1974) , using an emetic substance (lithium chloride, LiCl) with persistent effects on rodents (as demonstrated in laboratory and field settings; Martin & Storlien 1976; Gentle, Massei & Quy 2006), (2) Electronic deterrence by means of commercially-available, ultrasonic rodent repellent (Portavella, Depaulis & Vergnes 1993; Litvin, Blanchard & Blanchard 2007) primarily designed for domestic use and still needing a thorough testing in field conditions (Mason 1998, but see Schumake 1998). We first assessed whether egg size limits predation by black rat in easily accessible, undefended nests placed at ground level, and if so, examined the functional relationship between egg size and estimated predation risk (in the absence of parental protection). For this purpose, we used commercially available hen and quail eggs that reproduced the range of egg sizes laid by the five species of seabirds present in the study area (Table 2.1). In a second step, we used artificial nests with the most predated egg-size category to test whether

of the two artificial-deterrence methods provided an effective protection against rat predation. Because egg laying and incubation in seabird colonies may last for several weeks owing to asynchronous laying, we evaluated the effect of both methods for a period of five weeks (see Materials and Methods, section 2.2.3) and included an assessment of the persistence for the most effective method (egg deterrence by CTA) for an additional period of 17 days.

	Weight (g)		Length (mm)		Width (mm)		Shell Resistance (kg)	
	N	Mean ± s.e.	N	Mean ± s.e.	N	Mean ± s.e.	N	Mean ± s.e.
Quail	12	12.33±0.30	12	34.75±0.13	12	26.28±0.10	16	1.33±1.21
Hen Small	12	54.00±0.56	12	53.59±0.25	12	40.87±0.20	27	4.05±0.92
Hen M	12	59.75±0.73	12	56.19±0.33	12	42.88±0.26	10	4.34±1.04
Hen L	12	67.83±0.75	12	59,85±0.34	12	45.71±0.26	16	3.65±1.00
Storm Petrel *Hydrobates pelagicus*				28		21.2		
European Shag *Phalacrocorax aristotelis*				62.9		38.4		
Balearic Shearwater *Puffinus mauretanicus*				61.19		42.71		
Cory's Shearwater *Larus auduinii*				68.1		45.4		
Audouin's Gull *Calonectris diomedea*				62.2		43.3		
Yellow-Legged Gull *Larus michahellis*				69.8		48.2		

Table 2.1. Morphological features of hen and quail eggs used for the experiments, and seabirds that nest in Sa Dragonera Islet1.

2.2 Materials and methods

2.2.1 Study site

The experiments took place in Sa Dragonera, a small (288 ha) islet located 800 m offshore Mallorca Island (Balearic Archipelago; Fig. 2,1). The islet (4 km length and 1 km maximum width) shows a rough topography, with smooth hills facing south and sharp cliffs in its north face, and a skeletal calcareous substrate. Its climate is semiarid Mediterranean, with low annual rainfall (350 mm) and warm annual mean temperature (17-18 ºC; González & Navarro 2003). Its vegetation is

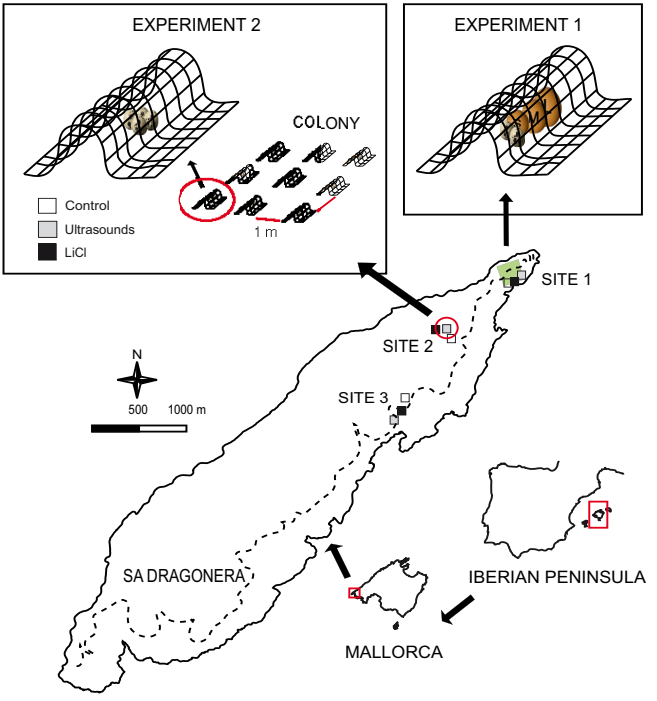

Figure 2.1. Study area and the three experimental sites in Sa Dragonera Islet. Experiment 1: 30 artificial nests containing different size eggs were set in an area (large green square) in Site 1. Experiment 2: In sites 1 to 3, three colonies of nine nests (distributed as shown in the left inset) were assigned one of treatments (i. e. one treatment per colony; open squares: control; grey squares: electronic deterrence; black squares: chemical deterrence).

dominated by sclerophyllous garrigue, with *Pistacia lentiscus, Phyllirea angustifolia* and *Olea europea* as most frequent species, interspersed with patches of Aleppo pine (*Pinus halepensis*) forest and coastal scrub. Due to its central location in the Mediterranean Sea (Fig. 2,1), its rough topography and a history of scarce human presence, Sa Dragonera is an ideal location for nesting seabirds. It was declared as a Special Protected Bird Area in 1979 and, since 1995, has been designated as the marine-terrestrial Natural Park of Sa Dragonera.

Within the north-eastern part of the island, we selected three study sites

with comparable topography and vegetation, and contrasting abundances of nesting yellow-legged gulls (*Larus michahellis*, gulls hereafter; Fig. 2.1). Site 1, situated nearby the Tramuntana Cape, had the highest density of gull nests and was situated in the vicinity of a colony of Audouin's gulls (*Larus audouinii*). Site 2, located mid-way between Sites 1 and 3, had a low density of gull nests. Site 3, situated nearby the Park's port and Information Centre, showed an intermediate density of gull nests, and was probably subject to a higher level of anthropogenic influence (although such influence is strongly limited by the Park's strict regulations).

2.2.2 Effect of egg size on predation rate

Experiment 1 (effect of egg size on rat predation rate) took place at Site 1. In July 2007, we placed 30 artificial nests containing eggs of four different sizes at randomly-chosen locations across the whole gull breeding colony (minimum distance between nests = 10 m). The experiment started immediately after the gull breeding season (March to June, in Dragonera Islet; González-Mulet J.M. pers. comm.), when rats had already been in contact with natural nests and eggs for several weeks. Half of the nests were placed under shrubs and the other half in open ground without shrub cover. Artificial nests were protected from predation by gulls or other birds by a 50 x 20 cm strip of wire mesh (2 cm mesh-size), fixed to the ground on two sides to form a "tunnel", which was still accessible by rats.

Each artificial nest contained five eggs: three hen eggs of different commercial sizes (S, M and L) and two quail eggs (we used two instead of one, to reduce differences in profitability between quail and hen eggs). We estimated the egg mass of each type and size class by weighing (to the nearest centigram)

a subsample of the experimental eggs (N=12). On a different subsample, we also measured egg length and width (using a digital caliper with 1 mm accuracy), as well as shell resistance (using a Z100 Zwick Universal Materials Testing Machine®). Egg resistance was defined as the maximum weight (in kg) that the eggs could bear until the first noticeable crack in the shell (Table 2.1). After the set-up, artificial nests were observed daily over six days, recording the number of eggs consumed, broken or transported out of each nest; all of these categories were considered as "predated".

2.2.3 Effect of chemical and electronic deterrence on egg predation

Experiment 2 (effectiveness of chemical and electronic deterrents) took place in October and November of 2007, outside of the period of gull nesting, to avoid the confounding effects of natural egg sources. Within each of the three study sites, we set three artificial "colonies" (Fig. 2.1), consisting of nine artificial nests arranged in a 2 x 2 m grid (colony size: 16 m^2; minimum distance between colonies: 50 m). Each artificial nest contained four eggs of the most-predated size (quail eggs, see Results, section 3.2) and was protected by a wire-mesh "tunnel" as in experiment 1. The three colonies were located in areas with comparable topography and vegetation, and were randomly assigned to three treatments (one treatment each): a) control, b) chemical deterrence and c) electronic deterrence. Control treatment involved no further manipulation to protect the eggs (i.e. they were freely accessible to black rats). Chemical deterrence consisted of the injection of 0.5 ml of a 3M solution of LiCl into each egg, calculated to achieve a final concentration 0.15 M within the egg (Loy & Hall, 2002). Electronic deterrence consisted of the installation of a battery-powered "anti-rat" ultrasonic-wave emitter

(SC.10RC RADARCAN ®, 20 m^2 wave range) at the centre of the colony, which broadcast during the entire experiment.

The experiment started at the beginning of October 2007, and continued for four weeks. Every 3 to 5 days (depending on logistic constraints, mainly weather and sea conditions determining access to the islet), we visited the artificial colonies, counted and removed all eggs with any sign of predation (whether consumed, broken or simply moved out of the nest) and replaced them to maintain a constant offering of four eggs per nest throughout the experiment. At the end of the four-week period, we assessed in detail the effects of the treatments (control and deterrents) by monitoring egg predation daily and without replacement for 6 additional days.

To evaluate the persistence of the chemical deterrence effects and obtain a more robust assessment of the relationship between treatments and observed egg-predation rates (given the low number of replicates, N=3), we completed experiment 2 with a treatment shift (which was applied after the 34 days of treatment described above). For this purpose, eggs in the "control colonies" were replaced by eggs treated with LiCl (i.e., they became "control → chemical deterrence" colonies), and those in "chemical deterrence" colonies were replaced by untreated eggs (i.e., they became "chemical deterrence → control" colonies). Due to logistic constraints (poor weather conditions), these colonies could only be visited (and predated eggs replaced) three times after the treatment shift, with irregular periods between visits (9, 4 and 4 days). In order to compare predation rates measured at equal periods of exposure to predation (four days), we used only the last two post-shift measurements for the analysis, and compared them to the last two measurements in the previous part of the experiment (i.e., before the treatment shift). Hence, the time elapsed from the treatment shift to the first post-shift measurement used in the analysis was 9 days.

In site 1 (Tramuntana Cape), the treatment shift to chemical deterrence was performed in the electronic-deterrence colony instead of the control, because (1) no difference in predation rate was detected in the first part of the experiment between these two treatments, and (2) due to unknown factors, the control colony at that site showed a total absence of predation, which dissuaded us from using it for this final test (see Results, section 3.2).

2.2.4 Statistical analyses

The effect of egg size on egg predation (experiment 1) was estimated by fitting Generalized Linear Mixed Models (GLMM; GLIMMIX procedure, SAS v.9.2, SAS Institute 2000) to the final survival after the 6-day period (*survival*), and the number of days an egg remained in the nest until being predated (*days to predation*), respectively. The information was split in these two separate but complementary response variables, as the random *site* factor prevented the performance of a survival analysis. In the case of the *days to predation* analysis, we included the 'alive' eggs in a seventh category (day), hence, making the analysis as conservative as possible by including them in the minimum day of the unknown period after the 6^{th} day. We fitted separate models in which either egg width, weight or breaking resistance were included as explanatory, continuous variables, and obtained comparable results (high correlation between these variables precluded their inclusion in a single, joint model). Hence, we only show here the results with egg width as co-variable. We used the combination of error distribution and link function that provided the best model fit; i.e. a Poisson distribution and a log link for *days to predation* and a binary distribution and a logit link for *egg survival*. To ensure the best possible model we tested (by default) several covariance structures of the random effects (autoregressive, unstructured,

compound-symmetry, radial smoother, Toeplitz, standard variance…). We combined as well the testing of linear and/or quadratic terms for the continuous factors in the model. We retained the models with the smallest AICc.

The effect of chemical and electronic deterrence on egg predation (experiment 2) was analyzed in four steps. First, we analyzed the proportion of nests attacked by rats (i.e. those with at least one predated egg) within each artificial colony, throughout the initial four-week period, by means of a longitudinal analysis (Hedeker, 2010; GLIMMIX procedure, SAS v.9; SAS Institute 2000) with a binomial error distribution, a logit link, *treatment* as fixed, categorical factor and *time* (number of days since the start of the experiment) as a continuous covariate (analogous to a within-subject effect in repeated measures). We fitted a repeated measures model, where the replicate unit was the *colony* (included as a random effect), which was itself nested within *site* (included also as a random effect). We used a random-coefficients model for *time*, which involves a mean slope of change along time (*time* fixed effect) and random contributions of each colony to this common slope (*colony*time* random effect).

Second, the number of eggs that survived predation within each measurement interval (*survival*) was also modeled by longitudinal analysis, using a linear mixed model (MIXED procedure, SAS ® v.9; SAS Institute 2000) with *treatment* as fixed, categorical factor, *time* (as above) as continuous covariate, and random effects for *site* and *colony* (nested within *site*). In this case, and owing to the complexity of temporal effects to be included in the model (see below), we aggregated the data per colony (i.e., we analyzed colony-wise mean survival, instead of survival per individual nest) and subjected it to square-root transformation.

Unfortunately, we were forced to discard the data from the control colony at Tramuntana Cape as, due to unknown factors, there was a null predation

throughout the duration of the experiment, counter to expected results based on all observations and experiments in the area (see also below). While the GLMM models for the proportion of nests attacked could be fitted in the absence of these values, in the analysis for mean survival we substituted these data gaps by "neutral" values calculated using Steel and Torrie's covariate method (Steel & Torrie 1960).

Third, data on daily egg predation (last six days of the deterrence experiment) were analyzed by fitting a GLMM (as above) to the response variable *days to predation* (following the transformation y=x+1 to avoid the presence of zero values), with *treatment* as fixed factor, *site* and *colony* as random factors, an exponential error distribution and a logarithmic link function. The purpose of this analysis was to evaluate treatment effects using a more detailed measure of predation risk (i.e. daily predation, rather than total predation after 3-4 days).

Finally, we assessed the effect of the treatment shift using a pre-post analysis based on GLMMs (Hedeker 2010; proc GLIMMIX, SAS ® v.9, SAS Institute 2000). The number of eggs surviving predation (per nest) was modeled using a Poisson error distribution, a log link function, *period* (pre/post) and *initial treatment* (LiCl or control) as fixed factors, and *site* and *colony* (nested within *site*) as random effects. In addition, the evaluation of the shift "chemical deterrence → control" provided an estimate of the persistence of deterrence effects.

2.3 Results

2.3.1 Effect on egg size on predation rate

The majority of eggs (86%) were predated during the 6-days period; i.e. rats were able to handle, break and consume even the largest hen eggs (45.71 ± 0.26 cm width, Table 2.1). However, egg survival increased with egg size ($F(1,119)=9.37$; $P<0.005$), showing a 13-fold increase for L-size eggs relative to

quail eggs (Fig. 2.2). Days to predation was also size-dependent (F(1,119)=21.26; *P* <0.0001), increasing linearly from 2.95 days in the smallest eggs up to 4.61 in the largest.

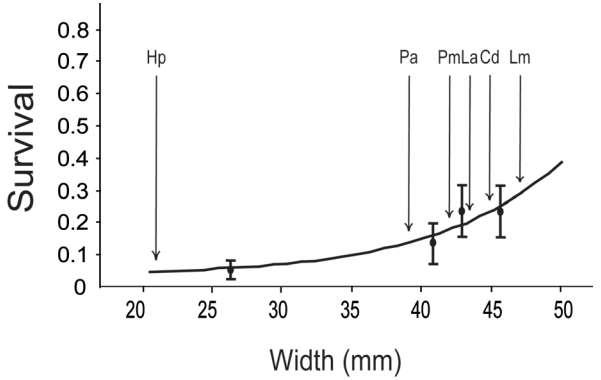

Figure 2.2. Effect of egg width on survival subjected to predation by black rats (*Rattus rattus*). Four different sized eggs (quail and S, M and L hen eggs) were offered during six days in undefended nests placed within a breeding colony of yellow-legged gulls. Arrows indicate the estimated survival probabilities of the eggs of six seabird species which nest in Sa Dragonera Islet (Hp: *Hydrobates pelagicus*; Pa: *Phalacrocorax aristotelis*; Pm: *Puffinus mauretanicus*; La: *Larus auduinii*; Cd: *Calonectris diomedea*; Lm: *Larus michahellis*).

2.3.2 Effect on chemical and electronic deterrence on egg predation

The proportion of nests that experienced rat predation increased sharply during the first fifteen days of the experiment (from 30 to 90% with all treatments pooled), until reaching an asymptote close to 100% of nests attacked (F(1,4)=6.36; *P* =0.652; Fig. 2.3 upper panel). The application of chemical and electronic deterrents did not reduce the proportion of nests predated (treatment: F(2,6)=1.65; *P* >0.05; days*treatment interaction not included in the final model; 2.3 lower panel).

Conversely, deterrence treatments reduced egg predation throughout the four weeks of the experiment (day*treatment effect, F(2,71)=10.17; *P* <0.001; day^2*treatment effect, F(2,71)=7.09; *P* =0.002). This was particularly true for the

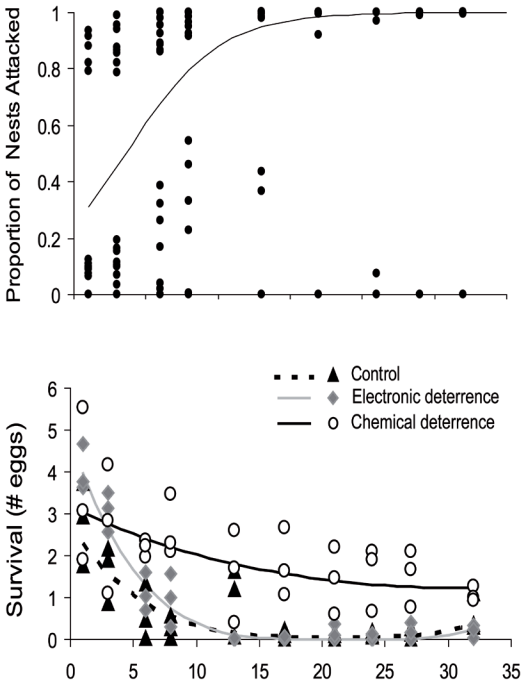

Figure 2.3. Effect of two deterrence methods on the predation rates of quail eggs. Electronic and chemical deterrence were tested for protecting artificial nests simulating seabird colonies. Artificial nests were grouped in "colonies" of nine eggs (see Fig. 2.1). Each data point shows the proportion of nests attacked or eggs consumed since the time at which the previous data point was measured (and all attacked eggs replaced). Upper panel: Nest predation (proportion of attacked nests) was monitored at regular intervals over time (days from the onset of the experiment). Line indicates the effect of time, as estimated from the GLMM model (all treatments pooled) and dots represent partial residuals. Lower panel: The effect of the three treatments (control, electronic deterrence and chemical deterrence) was measured for egg survival (the number of eggs, within each nest, that are still intact at the end of the observation period). Different lines indicate the effect of time for each treatment, as estimated from the GLMM model, and dots represent predicted values.

chemical deterrence treatment, which resulted in a significantly slower decrease in survival as compared to the control (t = -2.8; d.f. = 71; *P* =0.007 for the linear coefficient and t = 2.52; d.f. = 71; *P* =0.014 for the quadratic one) and electronic deterrence (t = -4.46; d.f. = 71; *P* <0.001 for the linear coefficient and t= 3.68; d.f.= 71; *P* <0.001 for the quadratic one) treatments. As a result, at the end of this phase of the experiment (day 30), colonies protected with chemical deterrence showed less egg predation than those with electronic deterrence (*survival*: mean difference= 1.01, t = 2.80; d.f.= 4; *P* =0.049) and marginally less than the controls (*survival*: mean difference= 1.03, t = 2.36; d.f. = 4; *P* =0.078). In contrast, electronic deterrence did not increase egg survival to rat predation, neither regarding its temporal pattern (t = 1.67; d.f. = 71; *P* =0.0997 for the linear coefficient and t =

-1.17; d.f. = 71; *P* =0.2479 for the quadratic coefficient) nor its final values (mean difference with control treatment= 0.09, t = 0.44; d.f. = 4; *P* =0.682).

More detailed analysis of egg predation carried out during the last six days of the deterrence experiment indicated that egg survival (*days to predation*) differed among treatments (F(2,67)=9.53; *P* <0.0005; Fig. 2.4). Eggs in chemical deterrence treatments survived longer than those in electronic deterrence (pairwise comparison: F(1,67)=13.64; *P* <0.005) and control (F(1,67)=13.65; *P* <0.005) treatments, between which there was not a significant difference (F(1,67)=0.26; *P* <0.6112).

The causal relationship between chemical deterrence and increased egg survival was confirmed by the treatment shift (significant period*initial treatment interaction; F(1,205)=21.58; *P* <0.0001), which showed a larger influence on the "control → deterrence" than on the "deterrence → control" treatment. Hence, following one month of chemical deterrence treatment, suspension of the treatment (i.e. a change to offering unmanipulated, control eggs) did not result in increased predation (F(1,205)=0.01; *P* >0.05) for at least 15 days (from

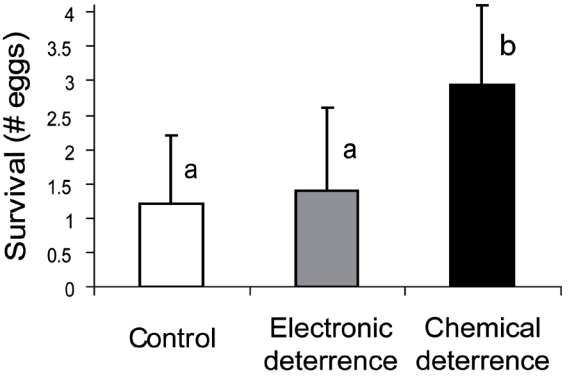

Figure 2.4. Effect of two deterrence methods on the survival of quail eggs to predation by rats. "Survival (# eggs)" is the number of eggs, within each nest, that are still intact after six days of exposure to rat predation (initial number of eggs = 4, mean ± standard error), following four weeks of deterrence treatment. Different letters indicate significant differences between treatments

the treatment shift until the last sampling). In contrast, colonies in the control treatment showed a significant decrease in egg predation after treatment shift (i.e. after being subjected to chemical deterrence; $F(1,205)=27.29$; $P<0.0001$).

2.4 Discussion

In our study system, eggs from all sizes tested were attacked and consumed by rats (i.e., we did not detect an upper-size threshold allowing eggs to escape predation owing to jaw-gap constraints, as suggested by Prieto *et al*. 2003). However, predation rate decreased with increasing egg size: larger eggs (which are more difficult to bite, handle and break, owing to their bulky dimensions, larger weight and more resistant eggshells) took longer to be predated and had higher survival at the end of our observation period (six days).

The positive effect of decreasing egg size on rat-predation risk suggests that, among ground and burrow/cavity nesting seabirds, those with smaller eggs will suffer larger egg-predation rates when facing rat invasions. Although our results are not directly applicable to real-world nests defended by adults, our results indicate that whenever nests are left unattended, smaller eggs will be more susceptible to predation (including both direct consumption at the nest and removal). This effect may be compounded by the smaller body size of the reproductive adults since smaller seabirds, which tend to produce smaller eggs, also show a reduced capacity to defend their clutches against rat attacks. This combination of effects may contribute to the higher sensitivity of smaller seabird species to rat invasions (Martin, Thibault & Bretagnolle 2000; Jones *et al*. 2008; Ruffino *et al*. 2009).

In a considerable number of cases, eggs were not consumed directly in the artificial nests, but dragged out of them and consumed outside, often in open ground. This behavior probably reflects a minimization of the risk arising from the

potential return of breeding seabird adult; i.e. a potential response of rats to nest defense by adults that may arise from their experience with nesting gulls at the study area.

If we assume that the observed predation rates represent a reasonable, though perhaps conservative surrogate of predation risk, we may conclude that invasions by the black rat are most likely to compromise the breeding success of the smallest seabird present in our study area – the storm petrel (*Hydrobates pelagicus*) in agreement with Ruffino *et al*. (2009) who only found evidence of rat impacts on the populations of this species. Other endangered seabird species on the island are likely to suffer considerable predation risk (from 0.29 egg^{-1} day^{-1} for Balearic shearwater to 0.28 egg^{-1} day^{-1} for Adouin's gull) whenever the adults leave the nest unattended. Our results therefore suggest that seabird egg (or body) size should be considered in the evaluation of the potential cost-benefits of rat eradication (e.g., Capizzi, Baccetti & Sposimo 2010; Genovesi & Carnevali 2011). However, caution is appropriate since numerous factors may condition both the effects of rat presence on nest predation (e.g., nest accessibility, nest defense by adults, rat abundance, availability of alternative food resources) and the likelihood that such effects would translate into changes in population dynamics (see, e.g., Igual *et al*. 2009).

As for the potential measures to mitigate egg predation by rats, only chemical deterrence resulted in a significant increase in egg survival, while electronic deterrence showed only a transient effect during the first week of the experiment (Fig. 2.3 lower panel). Because egg predation increased over time (Fig. 2.3 upper panel), as rats learn and get used to exploiting this new resource (which can be also expected in seabird nesting colonies, where eggs are available within fairly restricted areas for several weeks), the net effect of chemical deterrence was to slow down the buildup of higher predation rates. This effect was non-linear, so

that differences in egg survival between control and chemical deterrence colonies increased during the first two weeks of the experiment and remained fairly stable afterwards. By the end of the experiment (days 33 to 39), chemical deterrence colonies showed a three-fold increase in egg survival to predation, as compared to the electronic deterrence and control colonies (Fig. 2.4).

The potential use of chemical deterrence (generation of taste aversion using LiCl) in the wild has been previously explored in different settings, with positive results (e.g., to prevent egg predation by raccoons, *Procyon lotor*, Nicolaus, Hoffman & Gustavson 1982). This is the first direct proof, to our knowledge, of its effectiveness as a method for controlling seabird egg predation by rats – a necessary step given the species-specificity of the method (Paradis *&* Cabanac 2004). While reptiles and raccoons have been shown to have long-lasting aversive responses (up to 7 months; Nicolaus, Hoffman & Gustavson 1982 and Paradis *&* Cabanac 2004; respectively), conditioning on rats was only proven in the laboratory and over fairly short periods (up to 3 days; Loy *&* Hall 2002; Foynes *&* Riley 2004; De Brugada *et al*. 2005). Our data show, however, that after several weeks of conditioning, taste aversion provided protection to artificial colonies for at least two additional weeks. Further research would be necessary to evaluate, in practice, which specific settings may better serve the purpose of protecting seabird colonies against rat predation. For example, we would need to investigate whether interspersing within the breeding colony artificial nests with chemical deterrents should be done during the breeding period or before it starts. While the latter would have the advantage of creating aversion responses without disturbing the breeding pairs, it would also require a long-lasting persistence of such responses, which may be difficult to achieve under field conditions.

The results obtained in our experiment suggest a low suitability of electronic deterrence to mitigate egg predation in the wild. Our experiment was conducted

with commercially-available devices designed primarily for indoor use. The exposure of devices to outdoor conditions could have caused any equipment or battery malfunctioning on ultrasound volume or frequency. This factor is particularly important, as changes in sound frequency may completely alter the potential distress caused on rats (Sales 1991; Portavella, Depaulis & Vergnes 1993). Alternatively, rats may become accustomed to the device's emissions or learn to tolerate its distress in exchange for a reliable food reward (Barber 1915). While we cannot rule out any of these two possibilities, our experiment suggests that the use of available electronic deterrents is probably not effective for rat deterrence in outdoor conditions (see also Carlin 1969 and Howard, 1982 in Tesoro *et al*. 2000).

Our results show that larger eggs experience less predation by black rats, although none of the sizes we tested ensured a complete escape from it. The largest size tested, equivalent to that of the largest seabird species present in the study area (Audouin's and yellow-legged gulls), would still suffer a considerable predation rate (0.28 and 0.21 egg^{-1} day^{-1}) if left unattended. The two methods employed to mitigate such predation showed contrasting results: while the use of electronic deterrence only resulted in a limited and brief reduction of egg predation, the use of chemical deterrence showed a considerable reduction in egg predation (e.g., a three-fold increase in egg survival at the end of the experiment) that stabilized over time and persisted once the treatment ended for at least two additional weeks. Our results can be useful for the design of management programs in islands where seabird colonies are affected by rat invasions. Based on these results, we suggest that (1) seabirds laying smaller eggs (and/or having smaller body sizes) should be considered a priority, and (2) that chemical deterrence might be evaluated as a potential alternative to rat control programs whenever eradication is not possible or feasible.

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Chapter 3

Combined impact of multiple exotic herbivores on different life-stages of an endangered plant endemism, *Medicago citrina*

Impacto combinado de herbívoros exóticos múltiples sobre distintas fases vitales de una planta endémica amenazada, *Medicago citrina*

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3.1 Introduction

Plant recruitment is modulated by biotic and abiotic factors, which determine the survival of individuals between vital phases and ultimately condition population dynamics (Streng, Glitzenstein & Harcombe 1989; Bossard, 1991; Clark *et al.* 1999; Barberá, Navarro-Cano & Castillo 2006*)*. The analysis of such factors has therefore been a recurrent topic in population ecology from the early years of the discipline (e.g. Duncan 1954; Sacchi & Price 1992). Among biotic factors, the interaction between plants and herbivores has repeatedly been reported to be an intense modulator of plant population dynamics (e.g. Belsky 1986; Marquis & Braker 1994). Although the impact of herbivores is particularly significant during the initial stages of a plant's ontogeny (Hendrix 1988; Kauffman & Maron 2006; Bricker, Pearson & Maron 2010), their effects can be considerable over ulterior stages – saplings, juveniles and adults (Hester *et al.* 2000; Tanentzap *et al.* 2009).

Traditionally, plant-herbivore studies have focused on assessing the impact of a specific herbivore on a particular life stage of a focal plant species. However, recent work has started to address more complex cases, such as the impact of several herbivores on single plant-life stages (e.g., Hulme 1993; Louda & Potvin 1995) or that of single herbivores acting on multiple life-stages (Russell, Zippin & Fowler 2001). Different herbivores often show contrasting effects on the performance of consumed plants (Owen 1980; Rhoades 1985; Belovsky 1997), which may be mediated by contrasting impacts on different plant life stages (Maron & Kauffman 2006). Their combined action may result in either positive (Bakker *et al.* 2006), negative (Inouye 1982) or neutral (i.e. purely additive effects; Anderson & Paige 2003) accumulated impacts - or any combination thereof; e.g. Strauss 1991). In addition, the strong impact of a given herbivore type on particularly sensitive plant stages may determine *recruitment bottlenecks* that can limit plant

population dynamics – masking the putative effects of other herbivores in ulterior life-stages of the plant (Louda 1983, Louda & Potvin 1995).

These complex effects can be reduced or amplified by the concurrent effect of the (abiotic and biotic) environment. Aside from the more generic effects of habitat dependency (e.g. Kauffman & Maron 2006; Maron & Kauffman 2006, but see Russell, Rose & Louda *et al.* 2010), plant responses to herbivory have been shown to depend on resource availability (e.g. Hawkes & Sullivan 2001, Wise & Abrahamson 2007), physiognomic gradients (e.g. Louda 1982; Louda 1983; Reader 1992), safe-site availability (e.g. Maron & Gardner 2000; García, Obeso & Martínez 2005,) and community composition (Callaway *et al.* 2005; Baraza, Zamora & Hódar 2006).

Hence, in order to understand the conditions determining the effects of herbivores on plant performance and their ultimate bearing on plant population dynamics (Halpern & Underwood 2006), a deeper understanding of the effects of multiple herbivores on the various stages of plant development is required. Studies addressing such effects should ideally address the spatial context (e.g. habitat structure and/or community composition) in which they take place. Recent studies have extended their scope to deal with the differential effect of multiple herbivores (Strauss 1991; Hulme 1994; Gómez & Zamora 2000) and/or distinguish their effect on different plant life stages (Fagan & Bishop 2000; García & Ehrlén 2002; Horvitz & Schemske 2002) and others have analysed the effect of environmental gradients (Maron, Combs & Louda 2002; Maron & Kauffman 2006; Lau *et al*. 2008; Rose, Russell & Louda 2011) or density dependence (Parmesan 2000; Sullivan 2003) on herbivore impact. However, we are only aware of a handful of studies assessing the effects of multiple herbivores when acting on different life stages of their food plant (e.g. Lotze & Worm 2000; Vázquez 2002; Warner & Cushman 2002), as well as their interaction with spatial heterogeneity

in habitat and/or community composition (Louda 1982; Gómez, García & Zamora 2003; Traveset *et al.* 2003).

In this study, we used a series of field and common-garden experiments to estimate the relative role of different herbivores on different stages of the life cycle of a perennial plant. We focused on the impact of three exotic herbivores with different functional roles (a herbivore, a plant- and seed-eating omnivore, and a granivore) acting on three different life stages (seed, seedling, sapling and reproductive adult) of the endangered, endemic shrub *Medicago citrina* (Font-Quer) Greuter (Fabaceae). Specifically, we aimed to: (i) estimate the impact of the different herbivores on the different life stages of *M. citrina* and their cumulative effect on total plant recruitment (from seed to adult); (ii) identify "plant recruitment bottlenecks", i.e. plant life-cycle stages particularly prone to suffer herbivory impacts and therefore limit recruitment; and (iii) evaluate whether these effects vary between two habitat types.

Our study served also an applied purpose, related to the impact of exotic herbivores on insular plant endemisms. *M. citrina*'s status as endangered, protected species results from the combination of reduced geographic range (see below) and the putative impact of several exotic herbivores (goat, rabbit, black rat) introduced to its natural habitats (Juan 2002). By quantifying the impact of the main exotic herbivores present at our study site (the Cabrera Archipelago National Park) and comparing it to that of native herbivores, we present sound guidelines for the conservation of the existing species' populations and the design of future reintroduction attempts.

3.2 Materials and methods

3.2.1 Study site

Fieldwork took place at the Cabrera Island, situated just south of the island of Mallorca (Balearic Islands, eastern Spain) and included in the Cabrera Archipelago National Park (Fig. 3.1). Cabrera, the main island of the archipelago (1150 out of 1320 ha), is surrounded by 18 islets, 3 of which host small populations of the Western-Mediterranean micro-endemic *M. citrina* (see below for details). These islets have a calcareous lithology, and semiarid-warm Mediterranean weather (Emberger 1955), and are covered by Mediterranean garrigue under a discontinuous cover of Aleppo pine, *Pinus halepensis* L. (Rita & Bibiloni 1993). Cabrera's central valley (39°08'38.04''N, 2º56'10.92''W) hosted several agricultural plots which were abandoned in the mid-1960s and are now covered by tall grasses, thistles and spurges (*Euphorbia* spp.) interspersed with scattered, small bushes (hereafter referred to as 'grassland'). The study area (Fig. 3.1) comprised four independent sites located within these abandoned agricultural plots, at either valley-bottom areas of grassland or sloping areas colonized by open garrigue (2 sites each).

Medicago citrina (Leguminosae) is a perennial medium-sized woody shrub (≤3 m height) with a total distribution of <10 km^2 comprised of only 11 populations in small islets. It is distributed in the Balearic and Columbretes Archipelagos, and a few small populations on the Eastern coast of Spain (Juan 2002). Most of these populations are composed of a few hundred individuals and show a continuous decrease in the number of reproductive adults (Juan 2002). In Cabrera Archipelago, it is present in three small islets (<0.53 ha) situated around Cabrera: Ses Bledes, S'Estell de Coll and S'Estell de Fora (Palmer & Pons 2001; Juan *et al*. 2004). *M. citrina* differs from its two closest congeners (*M. arborea*

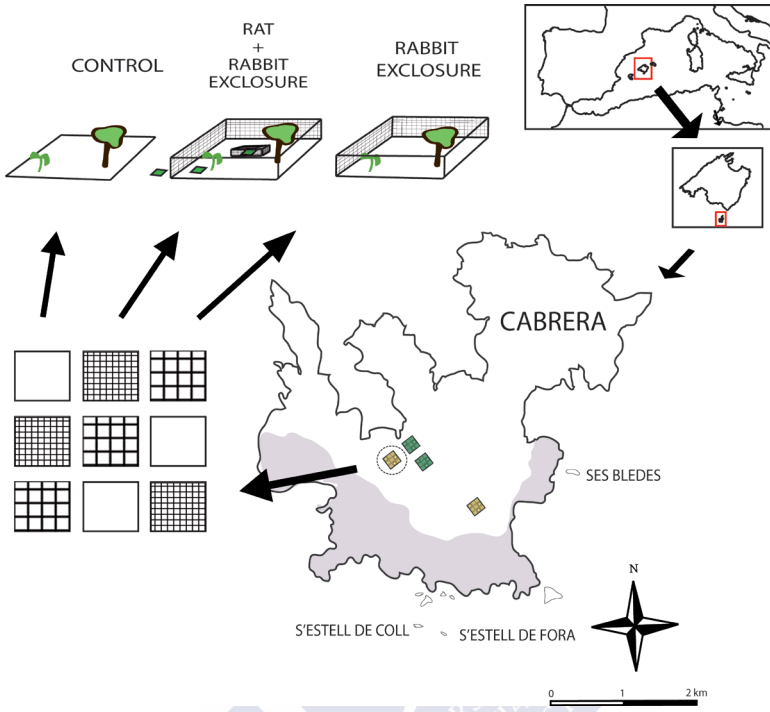

Figure 3.1. Location of study sites at Cabrera Island (Balearic Islands). There are two sites for each habitat (green: grassland; yellow: garrigue) containing three replicated plots of each of the three treatments (control, rabbit exclosure and rat+rabbit exclosure). Small and large plants symbolize different treatments of seedling- and sapling- predation experiments. At the 'rat + rabbit' exclosure, we have depicted also the seed-predation treatments (open trays outside and inside, plus 'rat + natives' caged tray).

and *M. strasseri*) in several morphological features (e.g. larger seeds and fruits, larger and tenderer leaves; González-Andrés *et al*. 1999; Sobrino *et al*. 2000) which tend to limit its dispersal capacity and make it more susceptible to natural enemies. It tolerates high levels of aridity, enabling it to survive in coastal rocky slopes with little to no soil (Pérez-Bañón *et al*. 2003; Juan *et al* 2004; Crespo *et al* 2007). It also shows a high regrowth potential, no vegetative reproduction and abundant seed production; although the seed set of small-islet populations may be lowered by a deficit of pollinators (Pérez-Bañon *et al*. 2003).

Similar to the rest of Balearic Islands, Cabrera has a long history of anthropogenically facilitated biological invasions (first human settlements date

from 2500 - 2300 BC; Alcover *et al*. 2001; Calvo, Guerrero & Salvà 2002). The invasion complex currently established on Cabrera Island includes three potential consumers of the study plant: a herbivore (the European rabbit, *Oryctolagus cuniculus* L.), a granivore (the house mouse, *Mus musculus* L.) and a plant- and seed-eating omnivore (the black rat, *Rattus rattus* L., Amengual 2000). Feral goats and sheep also roamed freely on the island until their elimination in the 1930s - 1940s (Alcover 1993) and 1991 (Frontera *et al.* 2000), respectively. The exotic scale insect *Icerya purchasi*, reported to attack *M. citrina* at Columbretes Islands (Juan 2002), has not been documented on Cabrera Island. Although we are not aware of any published information on *M. citrina*'s native granivores and herbivores, these probably include molluscs (mainly snails, including both native and exotic species; Altaba 1993), insects (mainly granivorous ants, which may also function as dispersal vectors, although the seeds lack elaiosomes and their large size, 20 mg on average, largely hampers transportation; Reader & Beisner 1991; Reader 1993) and granivorous birds (e.g. chaffinch, brambling, greenfinch and goldfinch; Traveset 1993).

Our study initially focused on the potential impact of the two most widespread herbivores, the European rabbit and the black rat (excluding the house mouse assuming its distribution to be restricted to the immediate vicinity of human settlements). Black rats have permanent populations on the two largest islands/ islets of the Cabrera Archipelago (e.g. Cabrera Island and Conillera Islet), while smaller islets experience sporadic colonisations followed by local extinctions (e.g. Illa de Ses Bledes, one of the islets hosting a *M. citrina* population; Palmer & Pons 2001). The National Park authority has applied successful rat-eradication programs in several small islets, while in the larger ones, eradication has not succeeded (Conillera Islet; Moreno 2009) or been attempted to date (Cabrera; J. Amengual, *pers. comm*.). European rabbits, native to the Iberian Peninsula,

were introduced into the Balearic Islands in the Talaiotic age (Alcover 1993). They show stable populations on Cabrera Island and Conillera Islet. To date, there has been no attempt to evaluate its impact on the native biota and/or control or eradicate its populations.

3.2.2 Field experiments

All experiments used four sets of exclosures installed in the study area to evaluate the impact of rodents (mainly rats, but also mice) and rabbits on native vegetation. Each of the four sets was installed at a different site, two of them in open garrigue and two in grassland vegetation (See Fig. 3.1). Habitat types (open garrigue and grassland) were selected to span the range of colonization sites available to *M. citrina* and variability in abundance of exotic herbivores (see below for details).

Each set of exclosures included 9 plots of 10 x 10 m, arranged to form a 3 x 3 square grid, with 1 of 3 possible treatments randomly assigned to each plot (thus making a total of 3 replicates per treatment per site): (1) Rabbit exclosure: plot fenced with wire mesh (1 m height, 5 x 10 cm mesh size buried at 30 - 50 cm depth), to prevent entrance of rabbits while allowing easy access to rats. Although the youngest rabbits (approx. one month age) could probably cross this fence, systematic mark counts and baited live-trapping (inside and around the plots) carried out during the three years previous to this experiment indicated that entrances were extremely rare (a single mark recorded in a single exclosure plot and no trapping, while marks and captures around the plots were abundant throughout the entire period). (2) Rat + rabbit exclosure: plot fenced with wire mesh (1 m height, 2 x 2 cm mesh size buried at 30 - 50 cm depth) to prevent entrance

of rabbits and rats, combined with bromadiolone-based toxic baits (Notrac Blox®) applied inside the plot (within baiting devices tailored to prevent the entrance of native vertebrates). Although occasional entrances were revealed by evidence of bait consumption, two-years monitoring of baited traps following the installation of the exclosures indicated no rat presence (no trapping after the first campaign, in which three individuals were removed). (3) Control: open plot.

At each site, abundance of both exotic herbivores (rabbits and rats) had been assessed by means of capture-mark-recapture during the two years that preceded the experiments (four sessions per year, Santamaría *et al*. 2007). Despite strong seasonal and moderate interannual variation, differences among plots remained comparable across the two-year period; hence, the data provide a good indication of spatial differences in herbivore abundances. As previously mentioned, we did not estimate mice abundance in our experimental plots because, according to local managers and practitioners (M. McMinn and J.A. Amengual, pers. comm.), they were only present nearby human settlements. Two isolated captures at the rat traps suggested, however, that they were able to enter the grassland plots (hence we set an extra treatment to account for their effect on seed predation; see below).

Seed predation

To evaluate the impact of the different (native and exotic) seed predators on seed survival, we offered groups of 20 seeds in plastic-mesh trays (10 x 10 cm) placed directly on the ground. At each site, we placed three trays (one per each of three treatments) in each of the rat + rabbit exclosures, as follows: (a) Control (open) trays were placed outside the exclosure, but in its immediate vicinity (< 5 m distance), and were accessible to all native (birds + ants) and exotic (rats + mice)

seed predators. (b) Rat-exclosure trays were placed inside the exclosure; hence, seed were only accessible to native predators (birds + ants) and, potentially, mice. (c) Rat + natives exclosures were placed to evaluate the impact of mice (as we suspected they could enter the rat exclosure but did not reach the bromadiolone bite due to their small size); trays were fixed on two wooden sticks (2 cm diameter by 20 cm long) impregnated with ant-repelling, contact insecticide (to exclude ants) and placed inside a wire-mesh cage (24 mm mesh size) that excluded birds but allowed mice to enter. Sticks held the trays at approx. 2 cm from the soil, preventing the access of ants (unless walking on them, from which they were repelled by the insecticide) but allowing easy access to the mice (without having to contact the sticks or encountering them before accessing the tray's content). All trays (4 sites x 3 treatments x 3 replicates = 36 trays and 720 seeds) were set in October 2005 and monitored monthly until September 2006 (except for January, March and April, when weather prevented access to the island). At each visit, we recorded the number of intact, partially consumed, damaged (attacked by fungi) and germinated seeds, and considered as predated the sum of those absent and partially consumed. Damaged seeds represented only a small portion (< 4%) of the seeds offered, and were excluded from the analyses.

Seed germination and seedling survival

To evaluate the effect of environmental variation (across the different habitats) on seed germination, and the subsequent effects of native and exotic herbivores on seedling survival (i.e. of seedling predation), we sowed 20 *M. citrina* seeds within each experimental plot (i.e. 20 seeds x 3 treatments x 3 replicates x 4 sites, making a total of 720 seeds; see above for a description of the different treatments in the plots). Seeds were sown in October 2005 at 1 cm depth in the soil and spaced regularly over a 20 x 30 cm grid (with specific positions assigned

at random). A wire mesh nailed to the floor (2 cm mesh size) provided protection against seed predators and was used to localize each individual seed (by means of a coordinate system). Germination and seedling survival were monitored at monthly intervals from November 2005 until September 2006, and revised again in subsequent years (April and May 2007 and March 2009) to account for long-term survival and delayed germination. However, the low germination rates observed prevented the analysis of seedling survival at the different treatments (see Results).

Seedling predation

To evaluate the effect of consumption by the herbivores on seedling survival, we germinated *M. citrina* seeds within plastic trays filled with soil in a greenhouse and offered them over a 4-week period in the experimental plots (5 – 10 seedlings per tray, 1 tray per plot, placed at a randomly-chosen place within the plot's surface, making a total of 282 seedlings). Trays were buried to level their surfaces with the surrounding ground, and their substrate was maintained wet using a diffusive irrigation system (a 100 ml bottle filled with water, buried next to the tray and connected to its substrate through a cotton wick that transferred water by capillarity) to prevent seedlings from withering during the four-week period. Trays were installed in April 2007 and monitored once after 28 days. Predated seedlings showed clear signs of herbivory, such as complete defoliation or consumption of stems at ground level.

Herbivory on saplings

To evaluate the effect of consumption by 2 of the herbivores (rats and rabbits) on sapling survival, we offered *M. citrina* saplings (2-year juveniles with woody stems and 60 ─ 170 cm height) in the experimental plots (two saplings

per plot, placed at randomly-chosen places within the plot's surface, making a total of 72 saplings). Saplings had been cultivated at a nearby site (the greenery of the National Park's Botanical Garden) and were planted by burying their pots at ground level. They were installed in April 2007 and monitored 35 days later to score sapling survival and herbivory damage (proportion of biomass removed, using a semi-quantitative scale).

Effect of simulated herbivory on reproductive success

Simulated herbivory was applied to 4-year old, adult individuals grown in a common-garden setting at Sóller Botanical Garden (Mallorca). In 2004, 68 2-year old individuals grown in individual pots from seeds collected at the Cabrera Archipelago were randomly interspersed and planted in the common-garden plot. Two years later, we measured the basal diameter of each individual (as a surrogate of plant size), grouped the individuals by size (17 groups of 4 individuals) and randomly assigned one individual from each group to one of the 4 simulated-herbivory treatments: 25%, 50% and 75% of canopy (leaves + branches) biomass removed, and a control (no clipping). Biomass removal treatments were chosen to span the complete range of herbivore pressure reported for the species (i.e. from little to no herbivory on small islets, to high to complete consumption by rabbits in the Columbretes Islands; Pérez-Bañón *et al*. 2003). In order to ensure a homogeneous removal of canopy biomass across the plant, we removed complete branches from the base to the tip of the plant, starting from a randomly-chosen branch amongst the four basal ones, and alternating removed and non-removed branches as required by the corresponding treatment (i.e. 25% removal = one branch of each consecutive four; 50% removal = two branches of each consecutive four; etc). Removed biomass was weighed and used to estimate total plant biomass (based on the fraction of biomass removed), which showed a

high correlation with the plant's basal diameter (r=0.77, P <0.005; control plants not included).

Simulated-herbivory treatments were applied at the beginning of the growth season (December 2006), and plants were monitored throughout the flowering and fruiting period (February-April 2007) to estimate reproductive effort and success (fruit and seed set). For this purpose, we recorded weekly the number of flower buds, closed flowers, unvisited open flowers, visited flowers and fruits in three branches per individual plant (marked before the onset of flowering, to avoid biases towards more productive branches). Unvisited and visited flowers were distinguished visually, since *M. citrina* flowers have an explosive tripping mechanism (i.e. the sexual column is released from the two-petal keel when a visiting insect presses the corolla tube for the first time, striking the stigma against it) that prevents pollination of unvisited flowers (McGregor 1976). On the last visit, we collected 30 (randomly selected) fruits per plant, and counted and weighed their seeds to estimate seed set.

3.2.3 Statistical analysis

All analyses were carried out using Generalized Linear Mixed Models (GLMM; procedure GLIMMIX) in SAS v.9 (SAS institute, 2000). Instead of pre-selecting a given error distribution and link function, we fitted all available error distributions and link functions and selected the one that minimized the residuals' dispersion and provided a better fit (based on the AIC score). All models included treatment and habitat (garrigue vs. grassland) as fixed factors, and site and plot as random factors. Post-hoc comparisons were subjected to sequential Bonferroni correction (Holm 1979).

Seed predation: Data were fitted to GLMM for seed survival (by the end

of the experiment) and for life expectancy of predated seeds (number of days from the beginning of the experiment to the predation of each seed, therefore describing predation rate) with binomial and normal error distributions and logit and identity link, respectively. Both models included an additional random factor to account for the covariance of the seeds belonging to the same tray.

Seed germination and seedling survival: Differences in seed germination between habitat types was analysed using a Fisher exact test using SPSS v. 16.0 (SPSS Inc. 2001) (after pooling all seeds across replicate plots due to the small number of germinated seeds). Seedling survival could not be analysed as a result of small sample size (low germination frequency).

Seedling predation: The survival of seedlings (offered in trays) was also fitted with a binomial error distribution and a probit link. We included tray as a random factor to account for the dependency among seedlings in the same tray.

Herbivory on saplings: All saplings attacked by herbivores suffered great biomass losses and died; hence, the only measure of herbivore damage analysed was sapling mortality. One of the treatments had no variance (all juveniles in the rat + rabbit exclosure survived; see below), which prevented the adjustment of parametric models to assess the effect of the three treatments on sapling survival. Instead, we used a 2 x 3 Fisher's exact test (Joosse 2011). Following the detection of significant differences among treatments, we performed 3 2x2 Fisher's exact tests to obtain pairwise contrasts between treatments, and adjusted the results using sequential Bonferroni correction. In addition, we evaluated the effect of sapling size on survival by fitting, only to data from the control and rabbit exclosure, a GLMM with plant size (number of leaves per plant) as a continuous covariate, treatment and habitat (garrigue vs. grassland) as fixed factors, site and plot as random factors, a binomial error distribution and a logit link.

The effect of simulated herbivory on reproductive effort (flower and fruit production per branch) and success (fruit and seed set, seed weight) was analysed by means of GLMMs with treatment as a fixed factor, basal diameter as a continuous covariate and plant as random factor. A normal error distribution and log link function was used for seed weight, a binomial error distribution and probit link function for fruit set, and a negative-binomial error distribution and log link function for flower production, fruit production and seed set.

Based on naive estimates (catch per unit effort, i.e. per trap and trapping nigh; CPUE hereafter) obtained by a previous capture-mark-recapture study (Santamaría *et al* 2007; average across all sampling sessions), we estimated the relationship between rat and rabbit abundances at each of the four sites and the mortality of *M. citrina* seeds, seedlings and saplings. Mortality estimates caused by rats and rabbits assumed additivity of effects (i.e. they were based on the difference between the mortalities recorded at the corresponding pair of exclosure treatments: rabbit = control – rabbit exclosure, rat = rabbit exclosure – rat + rabbit exclosure) and were regressed on herbivore abundance. Given the low sample size, these relationships are primarily shown to illustrate the effect of herbivore abundance upon the different life stages of our focal plant species, and should not be taken to provide robust statistical relationships.

3.3 Results

3.3.1 Seed predation

Only 16% of the 680 seeds were still present in the trays at the end of the experiment. 27 individual seeds were infected by mold, and therefore survival to seed predation was estimated on a total of 653 seeds.

Seed survival (by the end of the experiment) varied significantly between habitats ($F(1,2)_{=} 18.69$, $P < 0.05$), but not between treatments (treatment effect:

F(2,4)= 0.98, *P* >0.10, habitat*treatment effect: F(2,4)=0.55, *P* >0.10). Survival probability was much lower in grassland (0.89% on average) than in garrigue (24.97%).

In contrast, life expectancy (i.e. time to predation) of predated seeds varied significantly among treatments (F(2,4)=14.03, *P* >0.1), but not between habitats (habitat effect: F(1,2)=0.91, *P* >0.1; habitat*treatment effect: F(2,4)=2.81, *P* >0.1). In rat and rat + natives exclosures, life expectancy was comparable (140 ± 16 and 162 ± 15 days, respectively) and doubled that in open trays (59 ± 16 days; Fig. 3.2).

3.3.2 Seed germination and seedling survival

One year after planting seeds in the field sites, only 5% of the seeds had germinated. Seeds sowed in garrigue had more successful germination than those sowed in grassland (34 vs. 2 germinated seeds; Fisher exact test: *P* <0.0001). Seedling survival after one year was almost zero, mainly due to the

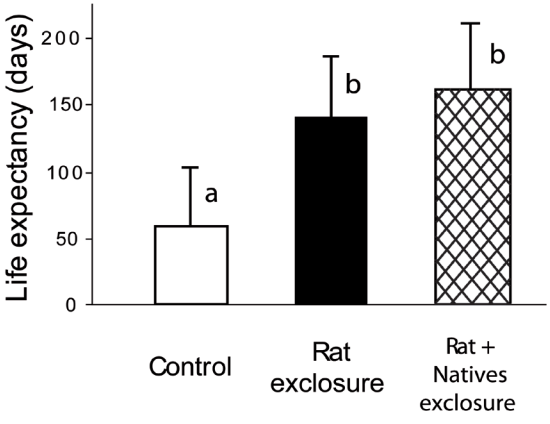

Figure 3.2. Effect of granivores on life expectancy of *Medicago citrina* seeds. 'Control' trays allowed access to all granivores. Life expectancy is represented by the number of days a seed remained in the tray until its predation. 'Rat exclosure' allowed access to birds, ants and mice. 'Rat + Natives exclosure' solely allowed access to mice. Different letters on top of bars indicate significant differences.

effect of summer drought (but also to predation: see below); however, three of the seedlings found in 2006-7 within rat + rabbit exclusions grew to middle-sized saplings by 2011.

3.3.3 Seedling predation

Seedling survival varied significantly among treatments ($F(2,4)=8.46$, $P<0.05$; Fig. 3.3). Survival increased around three-fold from the open control to the rabbit and rat + rabbit exclosures (30%, 83% and 98% survival, respectively). Assuming additive effects, rabbits, rats and native herbivores (insects and molluscs) were responsible for 53%, 15% and 2% of seedling mortality, respectively.

3.3.4 Sapling survival

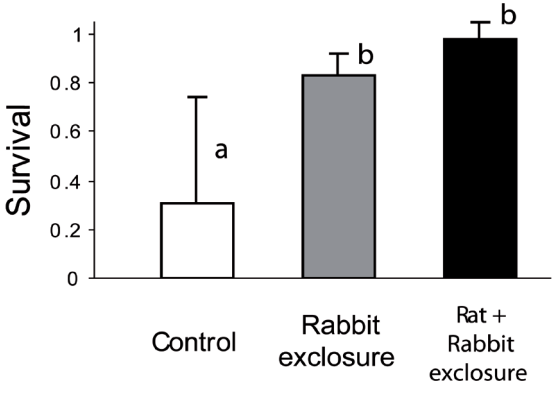

Figure 3.3. Effect of herbivores (rabbits, and rats) on survival to predation of *Medicago citrina* seedlings. Control plots allowed access to all herbivores (including rats and rabbits). 'Rabbit exclosure' allowed access to all herbivores but rabbits (i.e. rats and invertebrates). 'Rat + Rabbit exclosure' only allowed access to invertebrate herbivores (i.e. it excluded rats and rabbits). Different letters on top of bars indicate significant differences.

All saplings placed in rat + rabbit exclosures survived after one month, and we found no evidence of predation by native (invertebrate) herbivores. 2 x 3 Fisher's exact test indicated a significant effect of treatment on sapling survival ($P<0.005$). Subsequent 2 x 2 tests between pairs of treatments indicated that

the only significant difference was the 33% increase in survival from the controls to the rat + rabbit exclosures (P <0.005). Survival in the rabbit exclosures was intermediate and did not differ significantly from that in the other two treatments (P >0.1 in both cases; Fig. 3.4, left panel). Sapling survival increased marginally with the number of leaves (a surrogate of sapling size; $F(1,41)=3.69$, P =0.0668), but this relationship saturated for moderately large saplings (>300 leaves; Fig. 3.4 right panel).

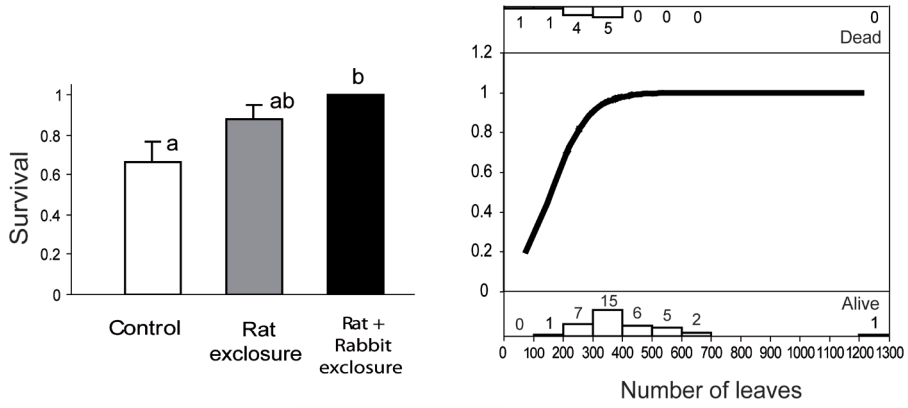

Figure 3.4. Effect of herbivores (rabbits and rats) on survival to predation of *Medicago citrina* saplings. Left panel: survival of saplings at three different treatments ('Control' allowing access to all herbivores, 'Rabbit exclosure' allowing access to rats and invertebrates, and 'Rat + Rabbit exclosure' allowing access to invertebrate herbivores. Different letters on top of bars indicate significant differences. Right panel: relationship between sapling size (estimated as the number of leaves) and survival in the control treatment (open to all herbivores).

3.3.5 Relationship with herbivore abundance

Estimates of the separate effect of each herbivore on *M. citrina* (assuming additivity of effects) only scaled to herbivore abundance for the sapling stage (Fig. 3.5). While both rat and rabbit increased their respective impacts on saplings proportionally to their abundance (R^2= 0.99, P <0.05 and R^2= 0.95, P <0.05, respectively), rat abundance was not significantly correlated to either seed (R^2= 0.02, P >0.1) or seedling (R^2= 0.02, P >0.1) mortality caused by rats. Similarly,

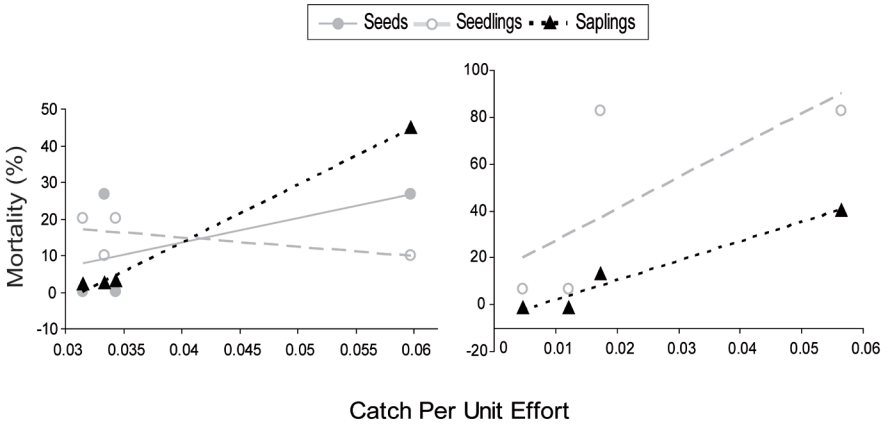

Figure 3.5. Effect of exotic herbivore abundance (left panel: rats; right panel: rabbits) on individual mortality of different life stages of *Medicago citrina*. X-axis: herbivore abundance (catch per unit effort = number of individuals per trap and night). Mortality estimates are based on the results of the different exclusion treatments, assuming additive effects of the different herbivores. Black lines and markers represent significant regressions; grey lines and markers represent nonsignificant regressions.

rabbit abundance was not correlated with seedling mortality caused by rabbits (R^2= 0.25, *P* >0.1). Correlations between the combined effect of both herbivores (control – rat + rabbit exclosure) and their cumulative abundance (number of rats + number of rabbits) showed comparable results: significant for sapling mortality (R^2= 0.98, *P* <0.05) but not for seed or seedling mortality (R^2= 0.17, *P* >0.1 and R^2= 0.01, *P* >0.1; respectively).

3.3.6 Effect of simulated herbivory on reproductive success

We estimated the effect of (simulated) herbivory on the reproductive success of adults with the assumption that, for adults, herbivory by rats and rabbits will not cause plant death (i.e. it will not represent a predation event, as it did for saplings and seedlings). The smallest basal diameter of the individuals at the onset of the experiment (1.13 cm) would result in 88% survival in the sapling-predation experiment (based on the results shown in Fig. 3.4, right panel, and the relationship between the basal diameter and the number of leaves of the plants used in the experiment) and, as most plants used in the experiment had

a diameter larger than 1.98 cm (77%), they would have shown a 98% survival in the sapling-predation experiment.

Flowering peaked in the third week of May, with a display of 9.52 ± 0.82 flowers per branch (average ± s.e). Almost every flower was pollinated during anthesis, indicating a lack of pollinator limitation in our common garden set-up. While simulated herbivory did not significantly affect flower production ($F(3,63)=0.37$, $P>0.5$), seed set (number of seeds per fruit: $F(3,29)= 0.20$, $P>0.5$) or seed weight ($F(3,28)= 0.56$, $P>0.5$), it resulted in a significant decrease in fruit set (54% less ripe fruits per flower; $F(3,52)=4.79$, $P<0.01$), which was comparable across all three herbivory treatments (i.e. 25, 50 and 75% removal; Fig. 3.6). Plant size (basal diameter) was strongly correlated with flower production ($F(1,129)= 22.28$, $P<0.001$), but not with fruit set ($F(1,52)$ 3.45, $P>0.5$), seed set ($F(1,698)= 1.38$, $P>0.1$) or seed weight ($F(1,28)= 0.09$, $P>0.5$).

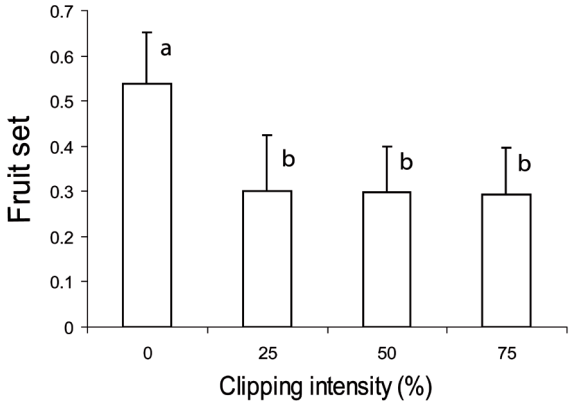

Figure 3.6. Effect of the simulated herbivory (clipping intensity) on the fruit set of *Medicago citrina* 'Clipping intensity' indicates the percentage of foliage (branches plus leaves) removed across the whole shrub canopy. Different letters on top of bars indicate significant differences (multiple comparisons after sequential Bonferroni correction).

3.4 Discussion

The different herbivores had complementary impacts on the different life stages of *M. citrina*, which may result in important cumulative impacts at the population level. While native herbivores appeared to pose little to no risk for *M. citrina*, rodents (black rats and mice) and rabbits severely reduced plant performance through their complementary impacts on its different life-stages. These included independent effects on different life-stages (seed predation by rodents, seedling predation by rabbits) that resulted in multiplicative increases on plant mortality, and concurrent effects on the same life-stage (sapling predation). Seed predation varied between habitats, while seedling and sapling herbivory effects did not. Differences in germination and seedling establishment could modulate herbivore impacts on plant recruitment (e.g. delayed germination could increase the impact of seed predation but also reduce the impact of seedling herbivory, through reduced appearance effects). In addition, the simulated-herbivory experiment showed that the reduction in flower production per plant (proportional to biomass removal, as flower production per branch did not differ between clipped and unclipped plants) is compounded by a strong decrease in fruit set, already observed at the lowest (25%) biomass-removal rate.

Predation by rats reduced the life expectancy of *Medicago citrina* seeds (Fig. 3.2), although after one year seed survival was comparable in open and excluded plots. This suggests the existence of different predation rates between rats and other granivores (largely mice, but also native granivores), whereby rats consume the available seeds more quickly. However, sustained predation by other granivores may suffice to deplete them within a single growth season (limiting the build-up of a dormant seedbank). At any rate, early predation by rats will severely reduce seed germination in the subsequent autumn, as it decreased seed life-expectancy (59 days) well below the minimum period between seed

production and germination (120 - 150 days, from April-May to October-November). All together, rodents had a large impact on seed survival, with overall survival rates (16%) much lower than the average, particularly for a species with large seeds (20 mg on average; Reader 1993) than the figures for the rest of life stages studied. These results support Maron and Crone's (2006) contention that, contrary to previous suggestions, granivore impact on plant populations is greater than that of other herbivores. In fact, rodents have been reported to be key determinants of seed fate and seed-bank dynamics across most bioclimatic regions (Heithaus 1981; Brown & Heske 1990; Hulme 1994; Hulme 1997) and a consumption of only 40% of the seeds produced may already lead to population declines (Bricker, Pearson & Maron 2010).

By contrast, seedling survival seemed to be unaffected by the presence of rats, while rabbits were responsible for a high mortality rates at this early stage. This pattern was different still for sapling survival, where rabbits had a greater impact than rats, but the combined effect of both herbivores was required to detect significant effects (which involved a 40% reduction in sapling survival). In summary, we detected two important bottlenecks at early stages of plant ontogeny; one caused by rodents (through seed predation) and one caused by rabbits (seedling survival), indicating that their combined action can impose a severe constraint on plant reproduction. This early risk is later moderated for small saplings, and disappears for large ones (>300 leaves). Admittedly, demonstrating the impact of herbivores on plant individuals does not lead to a complete understanding of their effect on plant population dynamics (Maron & Crone 2006), yet having focused on lethal effects, we can expect them to translate to reduced population growth rates.

Once the plant is large enough to overcome this high mortality risk, herbivory effects are likely to be dominated by sublethal impacts, which might still lead to

changes at population level (Maron & Crone 2006). We focused on the effect on plant reproduction and found that flower production per branch was unaffected by biomass loss during the early part of the growing season – i.e. plants neither expressed a trade-off between reproduction and vegetative regrowth (e.g. Edwards 1985) nor over-compensated for vegetative-biomass losses with an increased reproductive effort (Obeso & Grubb 1993; Agrawal 1998). Hence, flower production per plant decreased in direct proportion to the amount of biomass removed. Additionally, fruit set decreased after defoliation and, because seed set (per fruit) did not change; the reduction in seed production per plant can be expected to double the proportion of biomass consumed by herbivores. Similar results have commonly been reported which show a negative effect of herbivory either on fruit (McCarthy & Quinn 1992; Tong, Lee & Morton 2003; Hladun & Adler 2009) or seed production (Lee & Bazzaz 1980; Islam & Crawley 1983; Marquis 1984; Lehtilä & Syrjanen 1995). This effect was not linked to a decrease in pollination efficiency (flower visitation did not differ among treatments); hence, the reduction in fruit output could be the consequence of a change in resource availability or distribution (largely mediated by fruit abortion; data not shown) as a response to herbivory. It is important to note, however, that the response of our experimental plants could be conditioned by the favorable environment in which they are grown (in terms of soil quality and water supply), and it may change considerably under field conditions. In addition, because we only monitored the plant's response during the same growth season in which we defoliated them, long-term responses could compensate or exacerbate (particularly, if herbivory takes place every year) those reported here.

The effect of multiple herbivores on plant performance and population dynamics have received increasing attention in the past two decades, and the existence of common interactions among multiple herbivore species and

complementary and synergistic effects of these different species is now widely acknowledged (Hulme 1996; Juenger & Bergelson 1998; Gómez & Zamora 2000; Hufbauer & Root 2002). Our study supports this evidence by providing an example of a synergistic effect of two different herbivores acting on different life stages of the plant cycle. In our system, the combination of rat and rabbit effects on early stages and the effect of herbivory on adult reproduction lead to an important decrease of plant recruitment in natural settings. Herbivore abundances that would cause moderate damage to the plant foliage (only 25% of foliage removal) would already translate into a reduction of 60% of fruit and seed production. This effect would be exacerbated by subsequent seed, seedling and sapling predation. Hence, for the moderate rat and rabbit abundances of Cabrera, herbivory would severely reduce the number of individuals surviving until reproduction.

Surprisingly, few of the herbivory effects studied differed between habitats or replicate sites (with the exception of seed predation, which decreased by 25% from grassland to garrigue, and sapling predation, which increased proportionally to rat and rabbit abundances; Fig .3.5). These differences could be further distinctive as a result of the differing rates of seed germination and seedling survival between habitats, which are likely to modulate the effect of the detected herbivory bottlenecks on plant demography (Bonsall, Van der Meijden & Crawley 2003). For example, low germination in grassland will exacerbate the consequences of stronger seed predation by increasing the period at which seeds are vulnerable to granivores. Both habitats do also differ sharply on resource availability (soil quality and water availability), a factor that has been reported to determine herbivory compensation (Hawkes & Sullivan 2001). Woody species, in particular, tend to show stronger re-growth responses to herbivory in resource-poor habitats (Hawkes & Sullivan 2001), which could help garrigue plants to better compensate for herbivory damage. Despite the lack of relationship found for seed

and seedling predation, density dependence of herbivore impacts on saplings agree with previous literature (e.g. Pearson & Callaway 2008) and indicates that herbivore abundance surveys may provide useful information for managers interested in mitigating their impacts on vegetation.

These results stress the importance of considering the combined effects of different herbivores and assessing their consecutive effects on the various phases of the plant's life cycle (flower and seed production, as well as seed, seedling and sapling survival). In established populations with large numbers of adults and recruits, such a study would be best approached through the assessment of cumulative survival probabilities, from seeds to adults (Jordano & Herrera 1995; Shea & Kelly 1998; Lázaro, Traveset & Castillo 2006). This possibility is precluded by the characteristics of our study system: an endangered plant putatively driven to extinction by the impact of the invasion complex to which the studied herbivores belong. Instead, we resorted to a series of independent, short-term experiments that served the triple purpose of illustrating the complementary impacts of the different herbivores on different life-stages, identifying the most sensitive ones, and evaluating the potential of exclosure plots as reintroduction sites.

Here we give a final note to the relative effects of *M. citrina*'s exotic and native herbivores, and the potential reintroduction of the species on Cabrera Island. We found negligible effects of native herbivores and granivores, as compared to those of small exotic mammals. Although measured impacts on plant performance do not necessarily translate to changes in population dynamics, our results suggest that the combined impact of herbivores may have contributed to the extinction of *M. citrina* on the largest islands of Cabrera's Archipelago (Rita & Bibiloni 1993; Juan *et al.* 2004). Furthermore, the bottlenecks imposed by both exotic herbivores would likely hinder future reintroduction attempts (see also Pérez-Bañón *et*

al. 2003; Mestre, González & Del Señor 2010). It is possible that, in *M. citrina* populations reaching a reasonable proportion of large individuals, the levels of seed/seedling/sapling predation and adult herbivory imposed by (moderate abundances of) rats and rabbits could be tolerated. The evidence presented here suggests, however, that reintroduction efforts are unlikely to succeed in the presence of moderate, and even low, abundances of these herbivores, owing to the small population size and the strong dependence of new populations on the early recruitment phases (seed production, seedling and sapling survival). Reintroduction efforts should address the control of both exotic herbivores or the mitigation of their impacts, and also make use of the habitat preferences and transition probabilities identified here. According to these, the open garrigue shrubland is the most adequate habitat for seed germination and provides the highest survival to seed predation. However, it is also the habitat where both herbivores are most abundant and where desiccation risk is probably higher. Measures to prevent or mitigate seedling and sapling predation will therefore be required, be it in the form of rat/mice/rabbit eradication or control, or by means of mechanical structures (such as fences or individual exclusions) that provide protection to the earliest life stages.

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Chapter 4

Rabbits, not ungulates, kill seabirds on a continental island hosting a multi-trophic invasion complex

Complejos de invasión multitróficos en islas continentales: la presencia de conejos amplifica el impacto del visón sobre las aves marinas, pero no la de ungulados

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4.1 Introduction

Biological invasions are disproportionally common on islands (e.g. 80% of documented bird and mammal introductions took place on islands, Ebenhard 1988) and their impact tends to be more intense there than on mainland ecosystems (Vitousek *et al*. 1997; Courchamp, Chapuis & Pascal 2003; Hilton & Cuthbert 2010). Moreover, because insular biotas tend to be less diverse than continental ones, they present a weaker resistance to biological invasions and are more sensitive to their effects (Loope & Mueller-Dombois 1989; Simberloff 2000). Biological invasions, either on islands or mainland, rarely occur in isolation. Instead, they often involve the successive introduction of multiple exotic species that establish different types of interactions, including antagonisms (predator-prey, plant-herbivore, pathogen-host; e.g. Iverson 1978, Imber, Harrison & Harrison 2000, van Riper *et al.* 2002), mutualisms (plant-pollinator, plant-seed disperser; e.g. Simberloff & Von Holle 1999 and citations therein), commensalisms (Grigorovich *et al.* 2001) or more intricate combinations thereof (Wiles *et al.* 1996; Roemer, Donlan & Courchamp 2002). As a consequence, invasive species may facilitate the establishment of additional invaders for whom they represent trophic resources or mutualistic partners, forming invasion complexes which may multiply their impact on native ecosystems - a process referred to as *invasional meltdown* (Simberloff & Von Holle 1999; Richardson, Pyšek & Carlton 2011). Two common examples of this type of effects are the establishment of exotic predators following the introduction of exotic prey (e.g. cats or mustelids favored by the introduction of rats or rabbits; Dilks 1979; Oliver, Luque-Larena & Lambin 2009); as well as the facilitation of small herbivores by larger ones (e.g. rabbits favored by cattle and horses grazing, which results in more palatable pasture and/or enhances the detection of and escape from predators– particularly at moderately to high nutrient-rich environments; Bakker *et al.* 2006; Bakker, Olff & Gleichman 2009).

Because small herbivores (most notably rats and rabbits) and small carnivores (most notably cats and mustelids) are amongst the most pervasive and damaging invaders of insular ecosystems worldwide (Courchamp, Chapuis & Pascal 2003; Lowe *et al.* 2000), these two effects deserve attention as potential drivers of biodiversity loss in such ecosystems.

Besides their importance for understanding the effect of invasion complexes on insular biodiversity, interactions among herbivores or between predators and herbivores may result in unexpected or counterintuitive responses to management actions (Courchamp, Chapuis & Pascal 2003). In the first case, for example, the control or eradication of small herbivores (e.g. rabbits) could be aided by the simultaneous control or eradication of larger ones (e.g. ungulates). The second case has received more attention, largely related to the phenomenon of *hyperpredation* - a case of apparent competition in which the high abundance of a primary prey indirectly causes the decrease of a secondary prey by maintaining a high population of a shared predator (Holt 1977; DeCesare *et al*. 2009; Blanco-Aguiar *et al.* 2012). In the case of invasion complexes, an exotic predator population is maintained by an abundant exotic prey, promoting the predation of the alternative, native prey species (Smith & Quin 1996; Courchamp, Langlais & Sugihara 2000; Roemer, Donlan & Courchamp 2002; Zhang, Fan & Kuang 2006; Bate & Hilker 2012). Paraphrasing Courchamp (2000), if we take these two effects together 'ungulates might be killing seabirds' through a cascade of effects involving the facilitation of rabbits that represent the primary prey of small predators that prey on seabirds during the nesting season.

In this work, we combine field observations (rabbit demography), field experiments (vegetation monitoring at ungulate and rabbit + ungulate exclosures, as well as control plots) and demographic models to evaluate the relative contribution of herbivore facilitation and hyperpredation to the dynamics of a four-

species invasion complex and its impact on the native biota of a small continental island (Sálvora Island, NW Spain). For this purpose, we tested the following hypotheses: (i) Large exotic herbivores (two ungulates: feral horse and red deer) facilitate small exotic herbivores (European rabbit) by reducing vegetation height and/or promoting the growth of more palatable species (annuals instead of perennials and/or grass + forbs instead of small shrubs). (ii) Owing to differences in their foraging mode and abundance, small herbivores have much larger impacts than large herbivores on native vegetation. (iii) Exotic predators (American mink) that consume native seabirds during the breeding season, but depend on exotic prey (European rabbit) during the rest of the year, are able to colonize the island and breed on it. (iv) As a consequence, the impact of the invasion complex on seabirds is mediated by hyperpredation effects. Besides testing these hypotheses, the purpose of our study (and, in particular, of the modeling exercise) was also to provide management guidelines to the National Park office, for the development of an integrated control program for the American mink – a priority management target at the island.

4.2 Materials and methods

4.2.1 Study site

The study took place at Sálvora Island, a small (212 ha) continental island situated 3.3 km off the western coast of Galicia (NW Spain: 42°28'07''N, 9º00'54''W) and included in the Atlantic Islands of Galicia National Park (Fig.4.1). The island has an oceanic climate (1183 mm rainfall, 14.3 º C average temperature; Martínez Cortizas & Pérez Alberti 1999) and a gentle relief, composed of a low central hill (73 m a.s.l.) surrounded by a mixture of granite boulders and sandy meadows. The hill is covered by a small stand of *Eucalyptus globulus*; the central

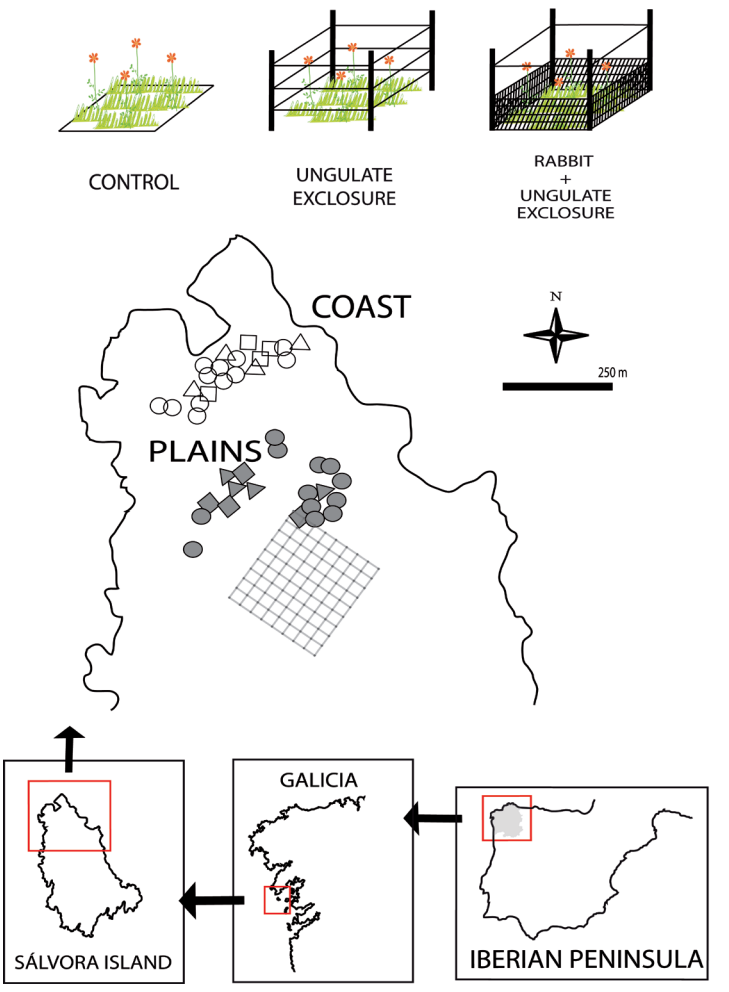

Figure 4.1. Location of study sites at Sálvora Island (Atlantic Islands of Galicia National Park). The grid represents the rabbit capture-recapture zone. The symbols represent the different plots of the herbivore exclosure experiment, where: circles = control plots, squares = ungulate exclosures, triangles = rabbit + ungulate exclosures, filled symbols = inland plots, empty symbols = coastal plots

meadows, by a mosaic of gorse (*Ulex europaeus*), bracken (*Pteridium aquilinum*) and grasses growing on organic-sandy soil; and the coastal fringe, by a mixture of rocky halophytes and beach/dune vegetation.

Field work took place in the northernmost part of the island (Fig.4.1), along

an inland-coastal gradient running from the inland meadows, dominated by forbs (*Erodium cicutarium*, *Anagallis arvensis*, *Anchusa calcarea*, *Echium rosulatum*) and shrubs (*Cistus salvifolius*), to secondary and tertiary dunes, dominated by small shrubs (*Armeria pubigera, Artemisia crithmifolia*, *Iberis procumbens*), halophytic succulents (*Crithmum maritimum*) and perennial grasses (*Elymus farctus*, *Ammophila arenaria*). The critically endangered species *Linaria arenaria* (Bañares *et al.* 2003) appears along the complete gradient at variable densities.

Sálvora Island hosts an invasion complex that includes a small predator (American mink *Neovison vison*, Schrebber, 1777), two large herbivores (feral horse *Equus caballus*, L. and deer *Cervus elaphus*, L.) and a small herbivore (European rabbit *Oryctolagus cuniculus*, L.). Brown rats (*Rattus norvegicus*, Berkenhout, 1769) and wood mice (*Apodemus sylvaticu*s, L.) are also assumed to be present on the island, mainly around human settlements (Mouriño 2002), but preliminary trapping trials during this study (100 live traps during 6 nights) showed that their abundance was negligible in the study area. While the time of introduction is unknown, it seems clear that all herbivores were introduced at least 40 years ago, when the last private owners started to use the island as a game reserve (Vilas *et al*. 2005). American mink was first detected in 2000 (Mouriño & Salvande, unpublished data) following the accidental escape and release of thousands of individuals from fur farms in the nearby mainland (Ruiz-Olmo *et al.* 1997). In the island, mink has been observed to feed on the most abundant species of gulls (the yellow-legged gull *Larus michahellis* (Naumann, 1840) and in less quantity, black-backed gull *Larus fuscus* (L.) (Molina 2009) during the breeding season. Recent studies of mink diet and prey remains on the islands of the whole Sálvora archipelago showed that mink feeds primarily on gulls during their breeding season - potentially causing the reduction in reproductive performance and subsequent decline of the most affected populations (Mouriño

& Salvande 2006). During the rest of the year, however, mink feeds primarily on other exotic (European rabbit) and native (fish, small rodents) prey (Romero 2009).

4.2.2 Abundance and demography of exotic species

Rabbit abundance and demographic parameters were derived from capture-mark-recapture (CMR) models based on data from six campaigns, each of them using a grid of 10 by 9 Tomahawk live traps (Tomahawk Live Trap Co. ®, Wisconsin, U.S.A.) arranged at 20 m intervals. The grid was situated at the inland extreme of the inland-coastal gradient used for the field work, where rabbit density was assumed to be maximal based on the advice of the warren service and preliminary observations. At this area, the sandy soil mixed with organic matter conforms an excellent substrate for burrow construction and vegetation growth is visibly impacted by the intense herbivory. From 2008 to 2010 (both years included), we carried out two trapping sessions per year (primary sessions), in spring-summer and autumn, each comprising 10 trapping nights (secondary sessions). Rabbits were individually marked with ear tags (LaQuick ®), sexed and weighed with a field scale (accuracy: 1 g).

Horse and deer populations were monitored by the Park wardens through occasional counts, although formal census campaigns were not undertaken. Mink population has been controlled and monitored in the island in 2007, 2009/10 and 2010/11 and density in the line coast of the island was 1.1 ind/ha. (Romero, unpublished reports [1,2,3]), On these reports, mink relative abundance was calculated for 500 m coastline sections and the number of captured individuals were also recorded (Fig. 4.2 lower panel).

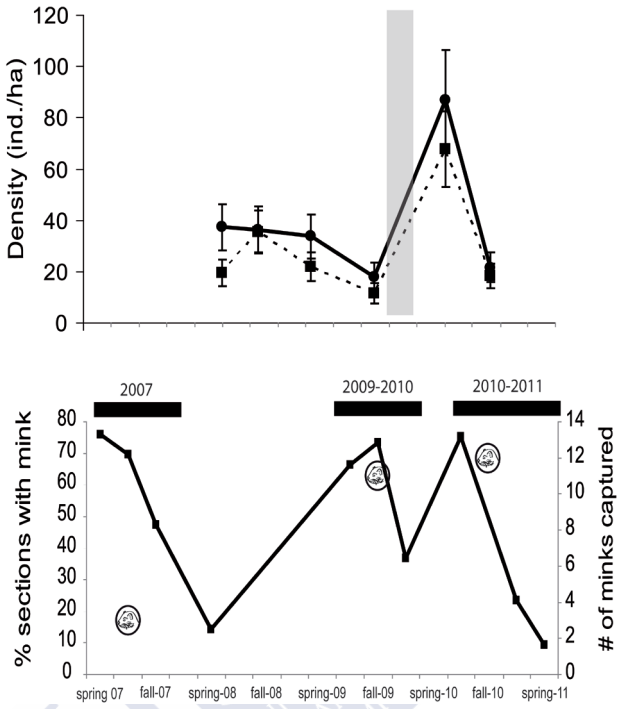

Figure 4.2: Abundance of exotic species at Sálvora Island. Upper panel: density of European rabbit (*Oryctolagus cuniculus*) at Sálvora Island over the three years of study (june 2008-december 2010). Solid line: females. Dashed line: males. Lower panel: abundance of mink (*Neovison vison*) on the same time period. Mink symbols indicate the number of individuals captured during the control campaigns (right axis). Solid line represents the percentage of coast sections with signs of mink presence. Thick horizontal lines indicate the duration of the different mink-trapping campaigns. (Romero, unpublished reports [1,2,3]).

4.2.3 Impact of exotic herbivores on natural vegetation

We studied the effects of exotic herbivores on the vegetation in the study area by measuring: (a) the cover, diversity and species composition of the plant community; and (b) the vegetative growth and reproduction of two species of conservation interest: the toadflax *Linaria arenaria* (DC.) and the endemic thrift *Armeria pubigera* (Desf.) Boiss. All measurements were carried out in a set of 40 permanent plots (3 x 3 m) randomly ascribed to one of three treatments: (a)

Control: open plots (*N*=24), (b) Ungulate exclosures: plots were fenced with barbed wire up to 1.5 m height, preventing access by ungulates but allowing rabbits to enter (*N*=8), (c) Rabbit + ungulate: plots fenced with wire cloth (0.5 m height, 20 mm screen opening size) buried in the ground to prevent access by rabbits and topped with barbed wire (as above) to prevent access by ungulates (*N*=8). The larger number of control *vs*. exclosure plots is related to our intention to use a 'ladder design', with 16 control plots switching to exclosure treatments (8 + 8) one year after the onset of the experiment. Logistic constrains related to bad weather conditions during winter prevented us from installing such exclosures, leaving the initial design unchanged. The 40 plots were installed in July 2008, with half of them respectively distributed at each of the extreme of the inland-coastal gradient described above and hereafter referred to as 'inland' and 'coastal' plots. In June 2008, before the installation of the exclosure fences, and in the two years that followed (June 2009 and 2010), we measured the cover, height and composition of the vegetation within each plot. Plant cover and species composition were measured using the line intersection method, i.e. recording the presence of every species present at each node of a grid of 11 by 11 points spaced at 25 cm (i.e. a grid that occupied the whole area of the exclosure). We also recorded the height of the tallest plant at each of such points. For each of the two species of conservation interest (thrift and toadflax), we estimated the size (cushion volume for thrift, plant height for toadflax) of ten haphazardly-selected individuals per plot. Thrift cushion volume was estimated assuming a hemiellipsoid shape; hence, V= (4Π /3*a/2*b/2*h)/2, where a and b are the major and minor axes of the basal ellipse, respectively, and h=height. For thrift, large herbivores often consume preferentially the inflorescences, rather than the vegetative parts; hence, we also recorded the number of inflorescences per individual. Since toadflax is an annual species and its abundance varied between years, we also recorded the number

of individuals per plot.

4.2.4 Statistical analyses

Capture-mark-recapture data were analyzed using MARK 6.0 (White & Burnham 1999). We fitted robust design models with Huggins' estimates (Alho 1990; Huggins 1991), as this allows for the inclusion of covariate effects. Our set of candidate models included different combinations of temporal heterogeneity, response to capture and weight effect on capture probability. To estimate the density of rabbits, we adjusted the area of the trapping grid by adding the area of a boundary strip according to the following equation:

$$A_{Adjusted} = A_G + P * W + \eth * W^2$$

where *W* corresponds to half of the average of the maximum distance between traps where rabbits were recaptured in the same primary session (Otis *et al.* 1978). We selected the model with the lowest AIC from our candidate model set.

To evaluate the effect of the exclosures on the vegetation of the plots, we used longitudinal analyses on the three-year data series. For this purpose, we fitted generalized linear mixed models (GLIMMIX procedure, SAS v.9.2 (SAS institute, 2000) on seven dependent variables: total plant cover, as well as the cover of perennial, annual, herbaceous and woody species (proportion of points per plot in all cases); diversity (as described by means of the Shannon-Wiener index, SWI; one value per plot) and plant height (measured at each observation point, i.e. 121 points per plot). GLM models included habitat as a fixed factor, plot as subject, time as fixed (longitudinal) effect and a random effect describing the among-plot variation in such longitudinal effect (random coefficients model). Because plant height was measured per observation point, we included 'point' as an additional subject (nested within plot) in the model. In all cases, AICc indexes of the full model and all nested sub-models were used to find the combination

of independent variables that provided the best fit. In addition, we compared the species composition of the different treatments and years using a multivariate correspondence analysis (CORRESP procedure, SAS v.9.2 SAS institute, 2000).

The size of the two species of conservation interest (thrift and toadflax), as well as the number of inflorescences of thrift, were also fitted to GLM models including the same factors and structure described above plus an additional subject for individual plants (nested within plots). Similar models were fitted to the abundance of toadflax, except for the absence of the 'individual plant' subject (since this variable was measured per plot). For the thrift, we fitted an additional random term, corresponding to individual experimental plots; and, for the number of inflorescences, we included plant size (as cushion volume) as an offset.

We used the error distributions and link functions that best fitted the data (see table 4.1). All the binomial models showed some degree of overdispersion, which was overcame by defining an inflated variance function, following McCullagh & Nelder (1989). Whenever treatment resulted in significant effects, we performed pair-wise comparisons between all levels, followed by Bonferroni adjustment to maintain an experiment-wise error rate of 0.05. Whenever the treatment*year interaction resulted in significant effects, we estimated simple effects (i.e. significant of the treatment factor within each year) and performed pair-wise comparisons only for the years in which significant treatment effects had been detected.

4.2.5 Demographic model

Based on the results of the previous sections and on parameters reviewed from the literature (Table 4.2), we built a demographic model to analyze the impact of mink on yellow-legged gull (gull hereafter) and the effect of rabbit abundance

	Response variable	Error distribution	Link function	Random effects	Subject	Overdispersion
Overall plant cover	cover fraction	binomial	logit	year	plot	inflated variance + overdispersion parameter
Annual plant cover	cover fraction	binomial	logit	year	plot	inflated variance + overdispersion parameter
Perennial plant cover	cover fraction	binomial	logit	year	plot	inflated variance + overdispersion parameter
Hebaceous plant cover	cover fraction	binomial	logit	year	plot	inflated variance
Woody plant cover	cover fraction	binomial	logit	year	plot	inflated variance
Vegetation height	cm	exponential	log	year	grid point within plot	
Diversity	Shannon-Wiener index	Gaussian	identity	year	plot	
Thrift growth	plant volume (cm^3)	lognormal	identity	Intercept year	plot individual	overdispersion parameter
Thrift inflorescence output	number of inflorescences (plant volume as offset)	lognormal	identity	Intercept year	plot individual	
Toadflax abundance	number of individuals per plot	lognormal	identity	year	plot	overdispersion parameter
Toadflax growth	square-root of plant height	Gaussian	identity	year	plot	

Table 4.1. Basic structure of Generalized Linear Mixed Models used to analyze herbivore impact on island vegetation. 'Overdispersion': method used to cope with overdispersed data, applying an inflated variance ($V = \hat{\imath}^{2} * \left(1 - \hat{\imath}\right)^{2}$) and/or estimating an overdispersion parameter.

Symbol	Parameter	Units	Values used for reference and control scenarios	Values used for sensitivity analysis
r_R	Growth rate of rabbit population	Ind.* ind.$^{-1}$ *year^{-1}	1.46	0.7-0.9-1.1-…-2.5
r_M	Growth rate of mink population	Ind.* ind.$^{-1}$ *year^{-1}	0.6	0.1-0.2-0.3-…-1
r_G	Growth rate of gull population	Ind.* ind.$^{-1}$ *year^{-1}	0.05	0.01-0.11-0.21-…-1.01
ε_R	Amplitude of seasonal variation in rabbit population growth rate	Dimensionless	6	1-3-5-…-19
ε_M	Amplitude of seasonal variation in mink population growth rate	Dimensionless	9	1-3-5-…-19
ε_G	Amplitude of seasonal variation in gull population growth rate	Dimensionless	9	1-3-5-…-19
K_R	Carrying capacity of rabbit population	Ind.	2000	500-1000-1500-…-4500
K_G	Carrying capacity of gull population	Ind.	2000	500-1000-1500-…-4500
γ_R	Predation rate of minks on rabbits	Ind.*ind.$^{-1}$*quarter^{-1}	16	2-6-10-…-38
γ_G	Predation rate of minks on gulls	Ind.*ind.$^{-1}$*quarter^{-1}	16	2-6-10-…-38
γ_O	Predation rate of minks on other native prey	Ind.*ind.$^{-1}$*quarter^{-1}	92	23-46-69-…-184
η_R	Preference of minks for rabbits	Dimensionless	9	0-2-4-…-19
η_G	Preference of minks for gulls	Dimensionless	9	0-2-4-…-19
η_O	Preference of minks for other native prey	Dimensionless	1	1
O	Number of other native prey available			92-184-276-…-920
μ_M	Mink migration rate	Ind.* quarter^{-1}	0.5	0.25-0.50-0.75-…-2.5
τ_R	Mortality caused by rabbit control program	Ind .*ind.$^{-1}$ *year^{-1}	0 to 0.9 at 0.1 intervals	0
τ_M	Mortality caused by mink control program	Ind .*ind.$^{-1}$ *year^{-1}	0 to 0.9 at 0.1 intervals	0
ε_{tR}	Season during which rabbit control is applied	Dummy variable	Spring-summer-autumn-winter	
ε_{tM}	Season during which mink control is applied	Dummy variable	Spring-summer-autumn-winter	
		Initial conditions		
R_0	Rabbit population size	Individuals	1000	1-251-501-…-2001
M_0	Mink population size	Individuals	1	0-5-10-…-45
G_0	Gull population size	Individuals	1000	1-501-1001-…-4501

Table 4.2. Parameters included in the demographic model. The right column provides the values used for the different scenarios.

thereof. The purpose of the model was double: (i) to evaluate the existence of hyperpredation effects in the rabbit-mink-gull system, and (ii) to compare the effects that different control strategies targeting mink and/or rabbit have on the mink, rabbit and gull populations. The three-species model was based in the equations developed by Courchamp (Courchamp, Langlais & Sugihara 1999, 2000) and implemented in Stella 7r ®. The model incorporated the effect of selection among prey species by the predator (Russell *et al.* 2009) and seasonality in their availability (i.e. gulls were available in summer, rabbits and other native prey throughout the year). Our initial idea was to incorporate the effects of ungulates on rabbit abundance; however, since our field results suggested a lack of such effects over the short term (2-3 years), we did not include it in the model.

The model included a description of the population dynamics of both prey species (rabbit *R* and gull *G*), based on logistic equations; a term describing the predation by mink (*M*) on gulls, rabbit and other native prey (*O*) that incorporates the mink's predation rate (γ) and its relative preference for each prey species (η):

$$\frac{dR}{dt} = \varepsilon_R r_R R\left(1 - \frac{R}{K_R}\right) - M\gamma_R\left(\frac{\eta_R R}{\eta_R R + \eta_G G + \eta_O O}\right) - \varepsilon_\tau \tau_R R \qquad [1]$$

$$\frac{dG}{dt} = \varepsilon_G r_G G\left(1 - \frac{G}{K_G}\right) - M\gamma_G\left(\frac{\eta_G G}{\eta_R R + \eta_G G + \eta_O O}\right) \qquad [2]$$

Mink population dynamics was also modeled as a logistic equation in which the carrying capacity was determined by the abundance of the different prey species

$$\frac{dM}{dt} = \varepsilon_M r_M M\left(1 - \frac{M}{\frac{R}{\gamma_R} + \frac{\delta_G G}{\gamma_G} + \frac{O}{\gamma_O}}\right) + \mu_M - \varepsilon_\tau \tau_M M \qquad [3]$$

and the predation rates exerted on each of them:

Equation (3) also includes a parameter describing mink immigration rate (μ_M). The model included a term resulting in seasonal variation in quarterly growth rate (r) which made r vary between a maximum value in two quarters (hereafter referred to as spring and summer) and a minimum value at the other two (hereafter referred to as autumn and winter). The amplitude of this variation was determined by the amplitude parameter ε, which determined the ratio between the maximum and the minimum values of the parameter being modeled. Gull availability for mink predation was described by a function that equaled 1 during the gull's reproductive period and 0 the rest of the year.

The equations describing the population dynamics of the two exotic species (rabbit and mink) include an additional term (τ) representing the effect of control programs, expressed as *per capita* mortality in order to account for their decreasing efficiency (based on trapping or baiting with toxic baits) with decreasing abundance of target species. The timing of such control programs was determined by means of a dummy variable (ε_τ) that determines the quarter in which the mortality caused by the control program (which equaled zero the rest of the year) equals the parameter τ.

The model was parameterized with values obtained in the study area (results of the upcoming sections and data from Romero, 2009) or, whenever necessary, derived from the literature (Table 4.2). Given the considerable uncertainty in the estimation of several parameters, however, we performed an extensive sensibility analysis in which each parameter was allowed to take 10 different values ranging from -100% to +100% of the value chosen to run the model simulations.

The first model scenario produced a baseline forecast of the evolution of the rabbit, mink and gull population under current conditions, in the absence of mink or rabbit control programs. All other scenarios evaluated the forecasted

effect of control actions targeting mink and/or rabbit. For each of these scenarios, we evaluated the effect that 10 different levels of control effort (*per capita* death rate from 0 to 90% of the population, in 10% intervals) had on the mink, rabbit and gull population. As indicator of the success of the different control programs, we focused on the short- and long-term fate of the gull population. All model simulations were run over a period of 125 years (500 quarters), although we only show results for the first 50 years because model dynamics was always stable afterwards.

4.3 Results

4.3.1 Abundance and demography of exotic species

The best fitting model for the rabbit population included (a) constant survival, dependent on rabbit weight, (b) response to capture, (c) no temporary emigration, and (d) no capture heterogeneity. Capture and recapture probabilities varied within primary sessions, but not among them. The model indicated a survival rate of 0.89 for males and 0.87 for females, which didn't vary between years or seasons but increased with rabbit weight. Rabbit density was almost constant until a sharp increase was observed in summer 2010, followed by a sharp increase in mortality that brought the winter density back to that observed in previous years (Fig.4.2, upper panel).

By 2008, deer and horse populations were estimated to include ca. 35 and 15 individuals, respectively. During the winter of 2009-2010, however, harsh weather conditions resulted in the death of most horses, leaving only 5 in 2010 and 3 in 2011. Although we have no information on changes in the deer population, the strong decrease in the number of horses probably caused a strong decrease of ungulate herbivory in 2010-11, as compared to that in previous years.

	Total Cover			Perennial species			Annual species		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;34	3.23	0.0519	2;34	1.78	0.1838	2;33	0.73	0.4898
Habitat	1;34	20.84	**<.0001**	1;34	5.16	0.0296	1;33	9.49	**0.0041**
Year	2;50	3.85	**0.0279**	2;50	7.25	0.0017	2;34	32.24	**<.0001**
Treat.*Hab.	2;34	4.27	**0.0221**	2;34	4.17	0.0241	2;33	3.73	**0.0347**
Treat.*Year	4;50	1.47	0.2263	4;50	0.55	0.7014	4;34	1.58	0.2032
Hab.*Year	2;50	2.23	0.1177	2;50	0.12	0.8876	2;34	2.05	0.1445
Treat.*Hab.*Year	4;50	0.58	0.6759	4;50	0.51	0.7310	4;34	1.34	0.2753

	Hebaceous species			Woody species		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;34	3.04	0.0609	2;34	0.02	0.9758
Habitat	1;34	15.06	0.0005	1;34	0.01	0,9314
Year	2;50	9.42	0.0003	2;50	1.76	0,1824
Treat.*Hab.	2;34	1.21	0.3117	2;34	0.58	0.5677
Treat.*Year	4;50	0.50	0.7349	4;50	0.19	0.9421
Hab.*Year	2;50	1.09	0.3441	2;50	0.24	0.7893
Treat.*Hab.*Year	4;50	0.01	0.9997	4;50	0.34	0.8487

Table 4.3. Generalized Linear Mixed Model results for the effect of herbivore exclosures on vegetation cover.

4.3.2 Impact of exotic herbivores on natural vegetation

Plant cover was higher at inland than at coastal plots (80 *vs*. 67%; F(1,34)=20.84, *P* <0.001; table 4.3). Herbivore exclusion did not result in a significant change in vegetation cover or diversity over the two years of monitoring (*P* >0.22 for the treatment*year and treatment*habitat*year interaction, for both variables; tables 4.3 and 4.4). No significant effects were detected either on the cover of annual species, perennial species (*P* >0.20 for the treatment*year and treatment*habitat*year interaction, for both variables; table 4.3), herbaceous species or woody species (*P* >0.34 for the treatment*year and treatment*habitat*year interaction, for both variables; table 4.3).

In contrast, vegetation height varied among treatments over the course of two years of exclusion (treatment*year interaction: F(4,51)=21.46, *P* <0.0001; table 4.4), increasing slightly over time at rabbit + ungulate exclosures, decreasing strongly at control plots in 2009 (but not in 2010, when it increased slightly),

	Vegetation height			Vegetation diversity (SWI)		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;34	18.66	**< 0.0001**	2;35	3.82	**0.0315**
Habitat	1;34	21.24	**< 0.0001**	1;35	86.48	**< 0.0001**
Year	2;51	45.71	**< 0.0001**	2;52	6.59	**0.0028**
Treat.*Hab.	2;31	18.85	**< 0.0001**	2;35	1.41	0.2577
Treat.*Year	4;51	21.46	**< 0.0001**	4;50	1.04	0.3956
Hab.*Year	2;51	24.16	**< 0.0001**	2;52	4.24	**0.0197**
Treat.*Hab.*Year	4;51	5.21	**0.0014**	4;52	0.56	0.6948

Vegetation height

Simple effects for treatment at different levels of habitat*year

Habitat	Year	d.f.	F-value	Pr > F
Inland	2008	2;51	10.69	**0.0001**
Inland	2009	2;51	27.14	**< 0.0001**
Inland	2010	2;51	19.18	**< 0.0001**
Coast	2008	2;51	19.64	**< 0.0001**
Coast	2009	2;51	9.73	**0.0003**
Coast	2010	2;51	5.37	**0.0076**

Least square means of each treatment at different levels of habitat*year

Habitat	Year	Treatment 1	Treatment 2	d.f.	t-value	Pr > t (adj.)
Coast	2008	Ungulates	Total	51	4.94	**< 0.0001**
Coast	2008	Ungulates	Control	51	-0.51	1.0000
Coast	2008	Total	Control	51	-5.81	**< 0.0001**
Coast	2009	Ungulates	Total	51	2.59	**0.0378**
Coast	2009	Ungulates	Control	51	4.37	**0.0002**
Coast	2009	Total	Control	51	1.68	0.2951
Coast	2010	Ungulates	Total	51	3.26	**0.0059**
Coast	2010	Ungulates	Control	51	2.08	0.1269
Coast	2010	Total	Control	51	-1.42	0.4834
Inland	2008	Ungulates	Total	51	4.58	**< 0.0001**
Inland	2008	Ungulates	Control	51	3.28	0.0056
Inland	2008	Total	Control	51	-2.05	0.1361
Inland	2009	Ungulates	Total	51	0.43	1.0000
Inland	2009	Ungulates	Control	51	6.43	**< 0.0001**
Inland	2009	Total	Control	51	6.10	**< 0.0001**
Inland	2010	Ungulates	Total	51	-5.11	**< 0.0001**
Inland	2010	Ungulates	Control	51	-0.96	**< 0.0001**
Inland	2010	Total	Control	51	5.68	**< 0.0001**

Table 4.4. Generalized Linear Mixed Model results for the effect of herbivore exclosures on vegetation height and diversity on Sálvora Island. Simple effects of treatment are shown for all significant Treat*Year effects. Significance values for least square means of vegetation height are Bonferroni corrected.

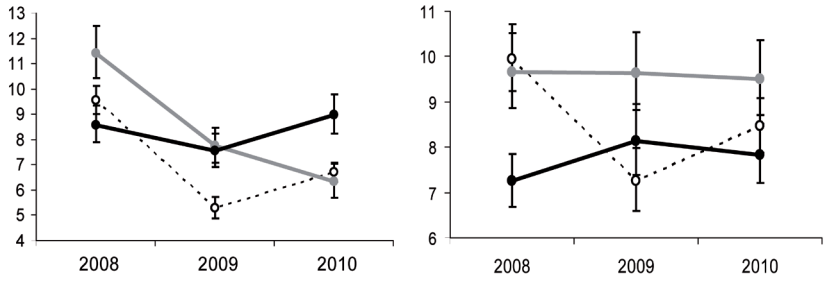

Figure. 4.3. Effect of herbivore exclusion treatments on vegetation height. Upper panel: inland sites; lower panel: coastal sites. Dashed line: control plots; gray solid line: ungulate exclosures; black solid line: rabbit + ungulate exclosures. Data from 2008 correspond to the original situation of all plots, i.e. before installing the exclosures. See Table 4.4 for significant values for least square means Bonferroni corrected.

	Volume			Density of inflorescences		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;36	1.70	0.1968	2;36	0.14	0.8669
Habitat	1;36	9.92	**0.0033**	1;36	11.86	**0.0015**
Year	2;49	16.55	**<0.0001**	2;48	39.67	**<0.0001**
Treat.*Hab.	2;36	0.41	0.6680	2;36	1.42	0.2559
Treat.*Year	4;49	2.08	**0.0976**	4;48	3.36	**0.0167**
Hab.*Year	2;49	1.87	0.1646	2;48	2.74	0.0743
Treat.*Hab.*Year	4;49	0.35	0.8430	4;48	1.28	0.2896

Simple effects for treatment at different levels years			
Year	d.f.	F-value	Pr > F
2008	2;48	1.04	**0.3599**
2009	2;48	0.61	**0.5477**
2010	2;48	2.24	**0.1171**

Table 4.5. Generalized Linear Mixed Model results for the effect of herbivore exclosures on *Armeria pubigera* size and reproduction on Sálvora Island. Simple effects of treatment are shown for significant Treat*Year interaction in the case of density of inflorescences.

	Abundance			Height		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;31	0.39	0.6836	2;30	1.07	0.3549
Year	2;8	3.46	**0.0828**	2;10	37.18	**<0.0001**
Treat.*Year	3;8	0.41	0.7526	3;10	3.60	**0.0536**

Table 4.6. GLMM results for the effect of herbivore exclosures on *Linaria arenaria* abundance and height on Sálvora Island.

and following an intermediate trend at ungulate exclosures. These effects varied between habitats (treatment*habitat*time interaction: $F(4,51)=5.21$, $P<0.01$; table 4.4; Fig.4.3), being more marked at the inland than at the coastal habitat.

Correspondence analysis showed that plant community composition varied more over time than as a response to the exclusion treatments (Fig.4.4). The first and second axes, which together explain 27% of the total variance, seem primarily related to temporal rather than treatment effects – in particular, the decrease in the annual herbs *Linaria arenaria* and *Erodium cicutarium* and the increase in the perennials *Cistus salvifolius, Lobularia maritima* and *Calendula suffruticosa* between the first and the second/third years (Fig.4.4). The third and fourth axes,

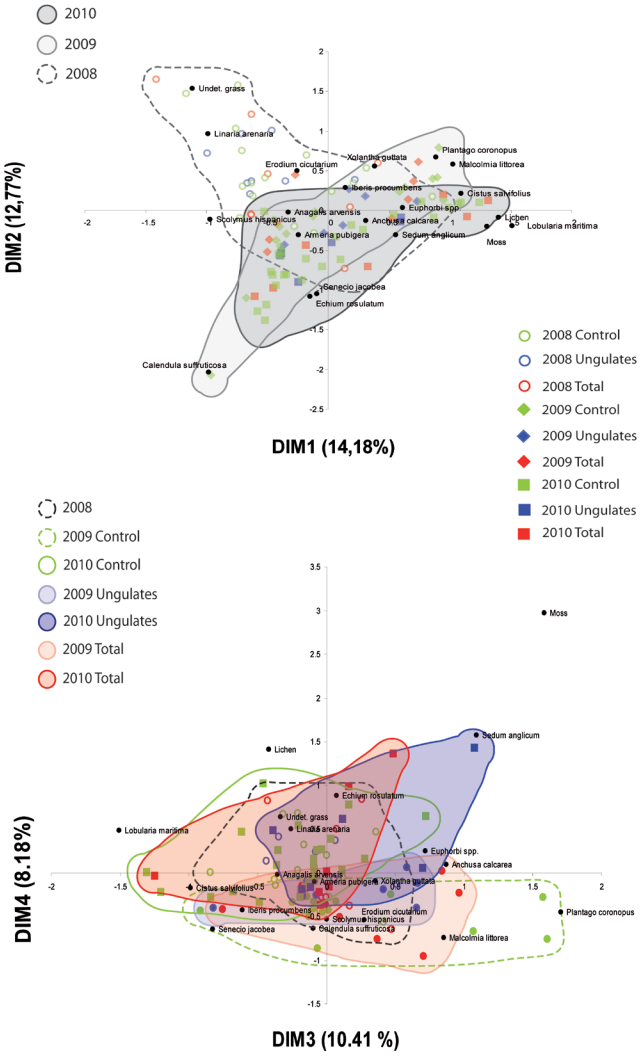

Figure 4.4. Plots derived from the correspondence analysis, showing the composition of the plant community at the different exclosure treatments during the three years of the study. Data from 2008 were collected before the onset of the treatments.

which together explain 19% of the total variance, do not seem to reveal either any consistent difference among treatments.

Thrift size, estimated as cushion volume almost doubled from 2008 to 2010 (average ± se = 7220 ±743 and 11087 ± 1078 cm^3 respectively, all treatments pooled). Cushion growth varied marginally among treatments (treatment*year significant; $F(4,49)=2.08$, P <0.098; table 4.5, Fig.4.5), being larger at rabbit + ungulate exclosures than at ungulate exclosures and control plots (which showed a comparable increase in cushion size). Thrift flower production (as number of inflorescences, correcting in the analyses for cushion volume) increased also over time ($F(2,48)=39.67$, P <0.0001; table 4.5). This increase varied among treatments ($F(4,48)=3.36$, P <0.017; table 4.5), being more pronounced at control plots than at both types of exclosures (Fig.4.6 left panel).

Herbivore exclusion did not result in a significant change in toadflax abundance over the two years of monitoring (P >0.68 for both treatment and treatment*year; table 4.6). Toadflax height, however, decreased significantly over time at control plots and ungulate exclosures (effect slices: $F(2,10)=41.48$, P <0.0001 and $F(1,10)=27.03$, P <0.0004, respectively; table 4.6, Fig.4.6 right

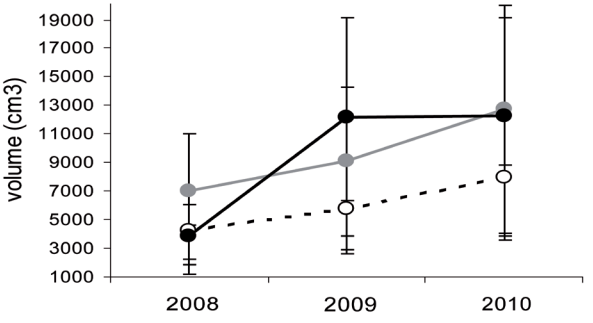

Figure 4.5: Effect of the exclusion of different exotic herbivores on the size of *Armeria pubigera* on Sálvora Island. Total exclosures: black solid line; ungulate exclosures: gray solid line; control plots: black dashed line. Data from 2008 were collected before the onset of the treatments.

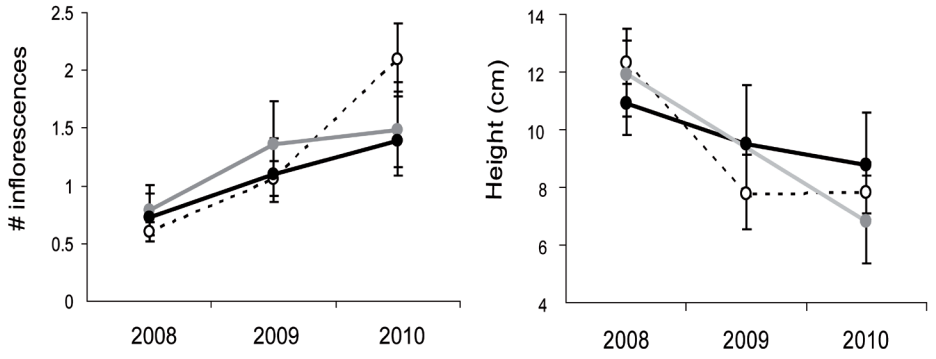

Figure 4.6. Effect of herbivore exclusion treatments on two species of conservation interest. Left panel: reproductive output (number of inflorescences) of thrift *Armeria pubigera*; the indicated values are the predicted means after correcting by the plant size, included in the model as an offset variable. Right panel: height of toadflax *Linaria arenaria*. Dashed line: control plots; gray solid line: ungulate exclosures; black solid line: rabbit + ungulate exclosures. Data from 2008 correspond to the original situation of all plots, i.e. before installing the exclosures.

panel), but not at rabbit + ungulate exclosures (effect slice: $F(2,10)=2.88$, $P>0.10$; overall effect of the treatment*year interaction: $F(3,10)=3.60$, $P<0.054$; table 4.6). Similar to what happened with vegetation height, the decrease in toadflax height at control plots leveled off in 2010 (when few horses remained alive).

4.3.3 Demographic model

Sensitivity analysis revealed that the parameters with the strongest effects on the three output variables (gull, rabbit and mink abundance) were (1) the growth rates of the three species, (2) mink's predation rate and prey preference, and (3) the carrying capacity of the rabbit population (Supplementary Material). In most cases, however, deviations larger than 50% of the value chosen for the simulations were required to cause a major change in model dynamics (e.g. a switch from the long-term persistence to the extinction of the gull, rabbit or mink population), i.e. smaller changes in these parameters only caused an acceleration or delay of the results reported here (Supplementary Material). Other parameters (such as the amplitude of seasonal variation in growth rates or the rate of predation on native

fauna) had negligible effect on the three output variables.

The reference simulation, under the current conditions (except for the absence of any control programs targeting American mink), predicts a sharp decrease of the gull and rabbit populations associated to the strong increase in the mink population (Fig.4.7). Both populations decrease strongly in the first 7-8 years and, despite the sharp decrease in the mink population at that point, become extinct by year 10. After that point, the mink population recovers to a low level owing to the immigration of new individuals.

Simulations with different levels of control of single species (either mink or rabbit) indicate that, in the long run, it is more effective to target rabbits than mink (Fig.4.7). Mink control only ensures gull population persistence until reaching its carrying capacity at high levels of efficiency (≥70% mortality) which must be maintained permanently. A sequence of high gull mortality followed by a recovery of the gull population is also predicted at intermediate control rates (20-40% mortality), but it would involve a considerable gull mortality during the first 30 years. Rabbit control, on the other hand, ensures gull population persistence at moderate levels of efficiency (≥30% mortality), albeit the initial decrease of the gull population may be quite severe (up to 50% of the initial number) and require a long recovery period (up to 100 years) at moderate control efficiencies (30 to 50% mortality). Over the long run, at all but the lowest control rates (>20% rabbit mortality), rabbits became extinct in 5-7 years and the mink population followed shortly – being maintained at low level by the immigration of new individuals afterwards.

The seasonality of the mink control campaigns had a considerable impact on its efficiency, in terms of mitigating the impact on the gull population. Control campaigns were much less efficient in autumn than in the other three seasons, and slightly more efficient in spring that in winter or summer – resulting in a four-

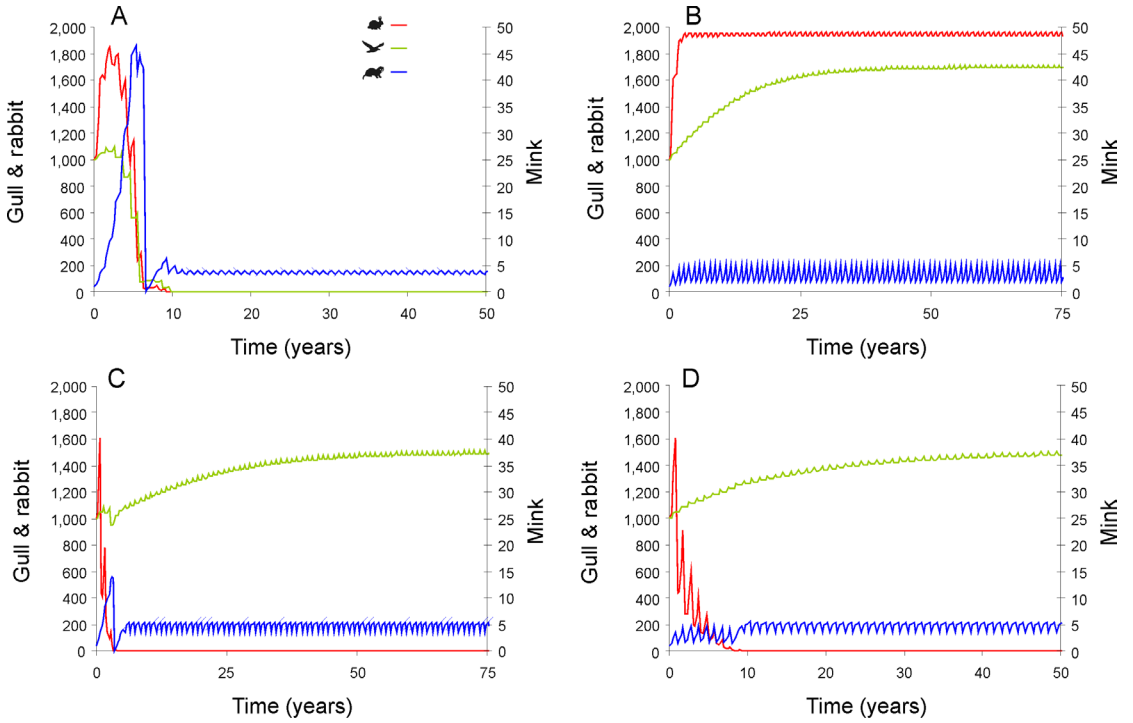

Figure 4.7. Examples of control strategies derived from simulations of the demographic model. (A) reference conditions (control of neither mink nor rabbit). (B) Permanent mink control, resulting in 75% mink mortality throughout the simulation period. (C) Temporary rabbit control, resulting in 75% rabbit mortality during the first four years. (D) Temporary control of both species, resulting in a 75% mink and rabbit mortality during the first 8 years. See Supplementary Material for the rest of control strategies.

fold difference in gull population size over the long run. This effect was largely related to a reduction in the predation on gulls by mink, since its overall effect on the mink and rabbit population was small. In contrast, the seasonality of the rabbit control campaigns had a considerable impact on the population of the three species (gull, rabbit and mink) over the short run (5-10 years), with stronger reductions in the decrease of the gull population for control campaigns carried over in spring and summer, but no effect in the long run (>40 years), following the extinction of the rabbit population.

The combination of mink and rabbit control might have the additional advantages of reducing gull mortality during the first years of the control program (by controlling mink predation) and shortening its temporal scope (which can be relaxed or abandoned once the rabbit becomes extinct). However, it involves a trade-off in terms achieving rabbit extinction – which takes increasingly longer as mink control efficiency increases and may become unachievable if the latter is too high.

As a summary of all these control scenarios, we present a choice of three management strategies (Fig.4.7). In all cases, a high but achievable efficiency of the control programs (75% mortality of the target species) has been assumed. Mink control achieves adequate results, in terms of conserving the gull population, but it must be applied permanently (Fig.4.7B). Rabbit control may be limited to a four-year program and still achieve the same objective, with a minimal cost in terms of initial mortality of the gull population (Fig.4.7C). Finally, an eight-years program of both rabbit and mink control could achieve the double objective of ensuring the long-term conservation of and reducing the initial mortality on the gull population (Fig.4.7D).

4.4 Discussion

Hyperpredation, but not herbivore facilitation, determined the dynamics of the invasion complex and its impact on the native biota of Sálvora Island. On the one hand, we found no conclusive evidence that large exotic herbivores (feral horse and red deer) facilitate small exotic herbivores (European rabbits) on the island. While some of the changes observed in the vegetation of excluded and control plots (such as the increased height at ungulate and rabbit + ungulate exclosures) suggest a facilitation effect, the exclusion of large herbivores did not favor the abundance of more palatable plants (e.g. herbaceous instead of woody species). More importantly, the peak in rabbit density following the massive mortality of feral horses in the winter of 2009-10 suggests a predominance of competitive effects (competition for food), at least in the short term (since rabbit densities came down to the previous baseline the following winter, probably owing to resource depletion). Furthermore, rabbits proved to have stronger effects than ungulates both on vegetation height and on the two species of conservation interest – which showed reduced vegetative growth (for thrift) and plant height (for toadflax) in plots subjected to rabbit herbivory. On the other hand, exotic predators (American mink) prey on native gulls during their breeding season, but depend on exotic prey (European rabbit) during the rest of the year – particularly in spring, when they represent 60-89% of their diet (Romero, 2009). Hence, the potential impact of the invasion complex on seabirds is mediated by hyperpredation effects: in the presence of rabbits, mink are predicted to drive gulls to extinction over a fairly short period of time (<10 years), while in their absence (e.g. following control programs) the gull population is predicted to persist despite moderate predation by mink. The main consequence, in management terms, is that control programs targeting rabbits may alleviate the need of sustaining mink control programs over unlimited time (see below).

The lack of short-term facilitation effects of ungulates on rabbits is coherent

with the characteristics of our study system, in which a high density of both large and small herbivores exploit a plant community of moderate to low productivity. Indeed, mean rabbit density (34.1 ind ha^{-1}) was larger than usually reported from continental areas (from 1.13 to 20.9 ind ha^{-1} at various European sites; Palomares 2001; Marchandeau *et al.* 2006; Serrano Pérez *et al.* 2008, Fernández-de-Simón *et al.* 2011) – although included within the varying range reported from invaded islands (e.g. 19 and 375 ind ha^{-1} at South Island and Whale Island, New Zealand; Moller, Clapperton & Fletcher 1997; Imber, Harrison & Harrison 2000). Similarly, the density of feral horses (16.5 ind km^{-2}) was in the upper range of those reported for feral horses across the world (1.3-27.8 and 0.1-35.4 ind km^{-2} at, respectively, three insular and 13 continental populations from the Americas, Europe, SE Asia and New Zealand, Linklater 2000; 2.01-6.40 ind km^{-2} at three populations from the Australian Alps , Dawson 2005). Owing to the intense foraging and the moderate site productivity, vegetation height – a key determinant of rabbit facilitation by ungulates, found to be related with food palatability and/or predator escape (Bakker, Olff & Gleichman 2009 and refs. therein), was much lower than reported in previous studies showing the existence of such facilitation. For example, treatment averages ranged from 7 to 12 cm, much lower than in the cattle and cattle + rabbit exclusions of Bakker (2009), where it increased from 10 to more than 25 cm in the first three years. It is worth noting, however, that a sward height of 7-12 cm resulted in decreased visitation and residence times of foraging rabbits (as compared to shorter swards), which was attributed to the effect of increased predation risk – since shorter swards provided lower rates of food intake (Iason *et al*. 2002). In our system, the effect of vegetation height on predation risk is probably limited by the virtual absence of terrestrial predators (including minks, currently targeted by control programs); hence, an increase in predation risk associated to the mink invasion could trigger or exacerbate such

effect. All in all, the existing evidence suggests that facilitation effects are not likely to influence rabbit abundance or demography in the short term, but we cannot rule out them (or an increase in their importance) over the long-term.

The impact of the invasion complex on native plants was driven by the effect of small herbivores. The composition and diversity of the plant community were both unaffected by the exclosure treatments, suggesting that ungulate and rabbit herbivory does not result in species replacement (even for annual species, which showed large changes in abundance in consecutive years). As for the two species of conservation interest, treatment effects on vegetative growth (thrift cushion volume and toadflax height) were primarily caused by rabbit, rather than ungulate, grazing. These effects are likely to build into demographic effects over the long run, since plant size is known to be a major determinant of survival and reproductive success. The limited effect of ungulate grazing is somehow surprising, as herbivory by this guild has been reported to affect plant composition, diversity, density, cover and height (McNaughton 1984; Milchunas, Sala & Lauenroth 1988; Milchunas & Lauenroth 1993; Putman 1996; Horsley, Stout & DeCalesta 2003; Côté *et al.* 2004; Bakker *et al*. 2006; Gill & Fuller 2007) – particularly on islands (Chouinard & Filion 2005). Once again, it is important to stress that the effects reported here have been monitored over a fairly short period of time (two years). While vegetation cover and diversity may show measurable responses to ungulate removal or exclusion over periods of two years (e.g. Donlan, Tershy & Croll 2002), such effects often involve prolonged lag periods (Kuijper *et al.* 2008) that may span from years (Tanentzap *et al.* 2009, 2011) to decades (Martin *et al.* 2010). At any rate, our results indicate that rabbit control programs, besides their beneficial effects on mink control, would reduce the main impact of the invasion complex on native plants.

While minks are able to recolonize Sálvora Island following control

campaigns and, once there, have been observed to breed on it, a recent analysis of their diet (Romero 2009) suggests that they would be unlikely to build a significant breeding population in the absence of exotic prey (rabbits). Indeed, gulls represent a significant part of mink diet during summer but, during the rest of the year, they rely primarily on rabbits – with occasional contributions of native prey (mice and shrews) which, given their abundance and small mass per individual, are likely to be of importance if minks become more abundant (Romero 2009). Diet data therefore suggest that the impact of mink on the gull population will be exacerbated by hyperpredation effects, whereby mink will be able to build a large population able to exploit gulls seasonally until driving them to extinction. This hypothesis was confirmed by model simulations, based (as much as possible) on parameters estimated from field data – and, more importantly, robust to large ranges of variation in all parameters. A key assumption of the model is that, during the gull breeding season, mink will show a preference for them over rabbits – a reasonable assumption, given the easy access to nesting adults and flightless chicks during this period, which makes gulls the predominant prey of mink in this and other gull breeding locations (e.g. Vidal-Figueroa & Delibes 1987). Such preference for native prey, together with the seasonality in its availability, triggers the hyperpredation effect – in an analogous way to the models of Courchamp, Langlais & Sugihara (1999, 2000) and Zhang, Fan & Kuang (2006), which did not model seasonality explicitly.

Our model differs from previous ones in two additional aspects, required to adequately tailor our study systems. First, we included a mink immigration rate to describe the arrival of new individuals from the nearby coast. This is an important point, because island isolation has been shown to be a key determinant of both the impact of mink on seabirds and the success of control or eradication programs (e.g. mink: Nordström *et al.* 2003, Nordström & Korpimäki 2004). Second, initial

conditions included a single mink individual – i.e., we modeled the build-up of the mink population. Both processes have a strong bearing on the temporal dynamics of the different simulations. On the one hand, starting the simulations from a small mink population size results in a high effectiveness of mink control programs, in terms of limiting the impact of gull populations (Fig.4.7B), but has a dual effect on rabbit control programs- which involve a limited contribution of mink predation to rabbit mortality (i.e., to the reduction of the rabbit population), but reach their objective (controlling mink abundance through a lack of native prey) without causing a too-severe episode of gull predation (Fig.4.7). On the other hand, owing to the continuous arrival of new individuals, mink control programs would have to be maintained permanently to achieve an effective conservation of the gull colony. Rabbit control, on the other hand, may achieve permanent effects in a short period of time (in our simulations, less than five years; Fig.4.7C). Taken these two effects together, an optimal control program could involve the simultaneous control of mink and rabbit– avoiding the transient period of high gull mortality associated to rabbit control programs and the need for permanent action associated to mink control ones. Indeed, inasmuch as our model predictions are realistic, a mixed control program could achieve permanent results in less than a decade (Fig.4.7D).

Although we have tried to tailor our model design and parameters to the study system, it is important to stress that we present a fairly simplistic model than cannot be taken to provide accurate predictions in absolute terms (neither in time nor in population numbers), but rather in comparative terms (among different scenarios). Moreover, counterintuitive responses such as those exemplified by our simulations could also involve some of the relationship not included in the model. For example, invasion by mink could trigger antipredator responses hampered by tall vegetation – resulting in herbivore facilitation effects not detected in their

absence. Another source of uncertainty is the extent to which mink are able to use the island, predating on the gull colony, without establishing a population on it – i.e. traveling back and forth from the nearby coast. Despite these and other uncertainties, a combined rabbit-mink program seems the most robust strategy given the available evidence – since it addresses all potential causes of concern and provides the additional advantage of reducing the main impact of exotic predators on native plants. Detailed monitoring of the complete invasion complex (mink, rabbit, horse and deer), as well as the gull population and native vegetation, should however be undertaken as a benchmark for the success of the control programs or any other management actions – ideally, under a well-planned strategy of adaptive management that includes the recurrent evaluation of newly available evidence.

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Supplementary Material

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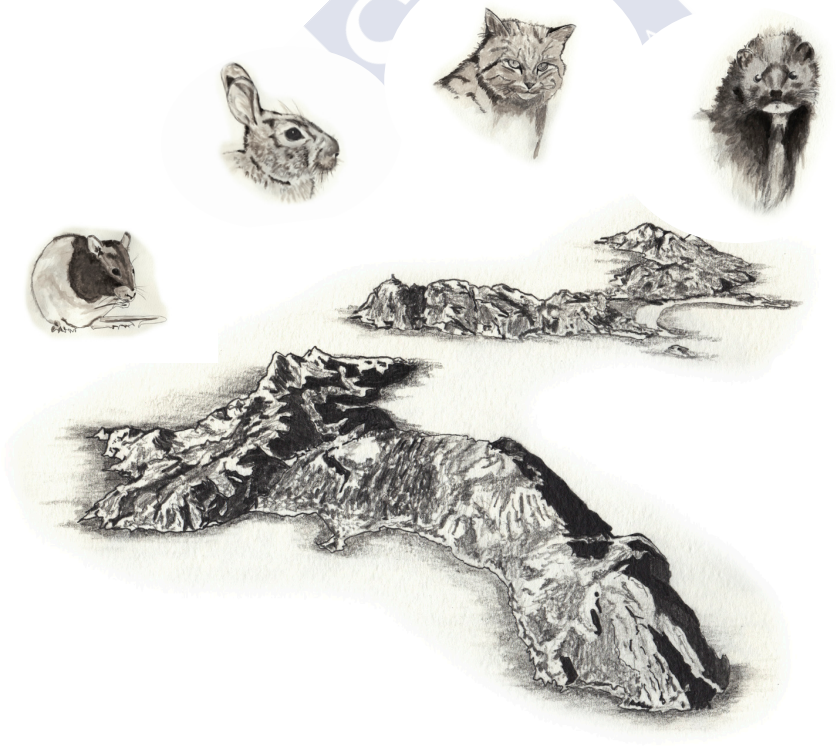
Chapter 5

Four are multitude: counterintuitive effects and the management of multi-trophic invasion complexes on a continental island

Cuatro son multitud: efectos inesperados del manejo de un complejo de invasión multitrófico en una isla continental



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5. 1 Introduction

Biological invasions are one of the compounds of global change and represent one of the main drivers of biodiversity loss (Vitousek *et al*. 1997; Ricciardi 2007). Their alarming prevalence on islands (e.g. 80% of documented bird and mammal introductions took place on islands, Ebenhard 1988) adds up to the fact that impact tends to be more intense there than on mainland ecosystems (Vitousek *et al*. 1997; Courchamp, Chapuis & Pascal 2003; Hilton & Cuthbert 2010). The evolutionary singularity of island biotas, most often evolved in isolation of natural enemies, resulted in absence of defenses against them (Bowen & Van Vuren 1997; Blackburn *et al.* 2004). Insular biotas tend to be less diverse than continental ones, which represents another cause for the weaker resistance to biological invasions and higher sensitive to their effects (Loope & Mueller-Dombois 1989; Simberloff 2000).

Single invasive species are rarely found on islands nowadays. Instead, they often involve the successive introduction of multiple exotic species that establish different types of interactions. In addition to their importance for understanding the effect of invasion complexes on insular biodiversity, these interactions often result in unexpected or counterintuitive responses to management actions (Courchamp, Chapuis & Pascal 2003). In particular, the reduction of predator numbers is considered a key conservation action in the management of many native vertebrates vulnerable to exotic predators. However, control attempts may affect non-target species through both trophic and competitive relationships. The three most prominent examples involve relationships between predator and prey (*mesopredator release* and *hyperpredation*) or between two predators (*competitor release*).

Mesopredator release takes place when the sudden removal of a predator reveals the importance of an inconspicuous intermediate predator, which, once

released from the predation pressure, leads to the strong reduction or even the extinction of a shared prey (e.g. Courchamp, Langlais & Sugihara 1999a; Crooks & Soulé 1999). It has been observed both under natural conditions (Rogers *&* Caro 1998; Myers *et al*. 2007; Brashares *et al*. 2010; Prugh *et al*. 2009), following anthropogenic disturbances such as habitat fragmentation (Crooks & Soulé 1999); or after the removal of (exotic) top predators by conservation programs – often resulting in the extinction of vulnerable prey species whose protection was aimed by such programs (e.g. Courchamp, Langlais & Sugihara 1999a and refs. therein). Management of invasion complexes with top predators and mesopredators is complicated further by a concomitant effect: the eradication of mesopredators might induce top predators to switch prey, increasing predation pressure on native prey (see Courchamp, Langlais & Sugihara 1999a and refs. therein).

Hyperpredation is a case of apparent competition in which the high abundance of a primary prey indirectly causes the decrease of a secondary prey by maintaining a high population of a shared predator (Holt 1977; Glen *&* Dickman 2005; DeCesare *et al*. 2009; Blanco-Aguiar *et al*. 2012). In the case of invasion complexes, an exotic predator population is maintained by an abundant exotic prey, promoting the predation of the alternative, native prey species (e.g. Courchamp, Langlais & Sugihara 1999b, 2000; Zhang, Fan & Kuang 2006; Bate *&* Hilker 2012; Roemer, Donlan & Courchamp 2002). While the impact of the exotic predator may be reduced by means of control programs targeting the exotic prey, caution must be exerted to prevent undesired effects similar to those described for mesopredator release – namely, that the eradication of exotic prey induces exotic predators to increase predation pressure on native prey (Courchamp, Langlais & Sugihara 1999, 2000).

Competitor release is a generalization of the mesopredator release effect

to other types of natural enemies. It takes place when, once released from an introduced natural enemy by human control, other introduced populations, initially maintained at low densities by that natural enemy, suddenly increase to levels such that they constitute a larger threat than the initial population ever did (Caut *et al*. 2007). For example, the eradication of rats from an island has been shown to trigger demographic explosions of competing mouse population (Caut *et al*. 2007 and refs. therein). Control levels and target specificity have a direct influence on the extent of this process: counterintuitively, the stronger and more specific the control (i.e. the stronger the effect on the targeted exotic species), the greater the increase in the abundance of the other exotic species.

Most studies address these dynamics separately, using theoretical approaches (e.g. Crooks *&* Soulé 1999; Courchamp, Langlais & Sugihara 1999a; Zavaleta 2002; Fan, Kuang & Feng 2005; Gehrt *&* Prange 2007; Rayner *et al*. 2007; Bergstrom *et al*. 2009; Russell *et al*. 2009; Dumont *et al*. 2010) or empirical observations (e.g. Rogers *&* Caro 1998; Courchamp, Langlais & Sugihara 1999a; Crooks *&* Soulé 1999; Fan, Kuang & Feng 2005; Gambino *et al*. 2007; Gehrt *&* Prange 2007; Rayner *et al*. 2007; Bergstrom *et al*. 2009; Russell *et al*. 2009; Dumont *et al*. 2010), in relatively simple systems with two exotic species and a single native one. In many insular and continental systems, however, invasion complexes include multiple predator and prey species with increasingly complex effects on native species and ecosystems (Sih, Englund & Wooster 1998). In such cases, conservation programs aimed at reducing or mitigating their effects on native species must face complex decisions that are likely to involve different types of counterintuitive effects.

In this work, we evaluate the impact of inter-specific interactions in a multi-species invasion complex with two top predators, a mesopredator and a herbivorous prey (Fig. 5.1), established at two joined continental islands belonging

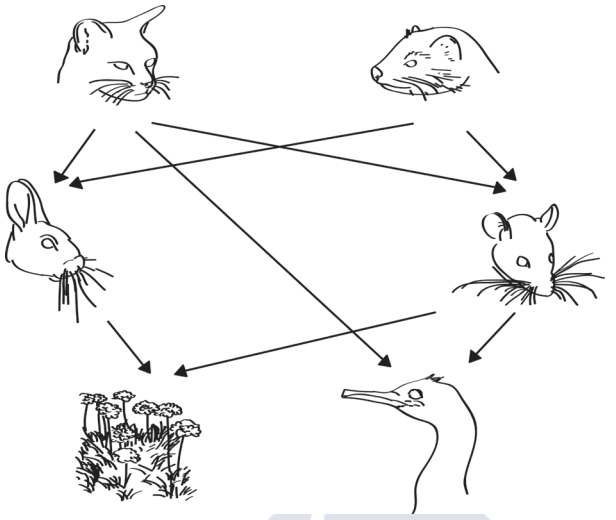


Figure 5.1. Potential interactions among the different species of the invasion complex addressed in this study. Top predators: feral cat and American mink. Mesopredator: black rat. Herbivore: European rabbit. Native seabird of conservation interest: European shag. Native plants of conservation interest: searose and Portuguese crowberry.

to the Cíes Islands archipelago (NW Spain) where it has a demonstrated impact on several native species. With the specific aim of supporting the existing conservation programs, we used a combination of empirical observations and demographic modeling to evaluate (i) the impact of the invasion complex on native species, and (ii) the effects of trophic and competitive interactions among invasive species on the expected responses of the invasion complex to different management actions. The results are used to both discuss the relative importance of the three types of counter-intuitive responses described above (mesopredator release, hyperpredation and competitor release) and provide guidelines for the management of insular invasion complexes. As indicators of the effect of the various management actions, we paid particular attention to the impacts of the exotic predators on European shag (*Phalacrocorax aristotelis* L.) and the exotic herbivores on two endangered plant species (searose *Armeria pungens* [Link] Hoffmanns. & Link and Portuguese crowberry *Corema album* [L.] D. Don.).

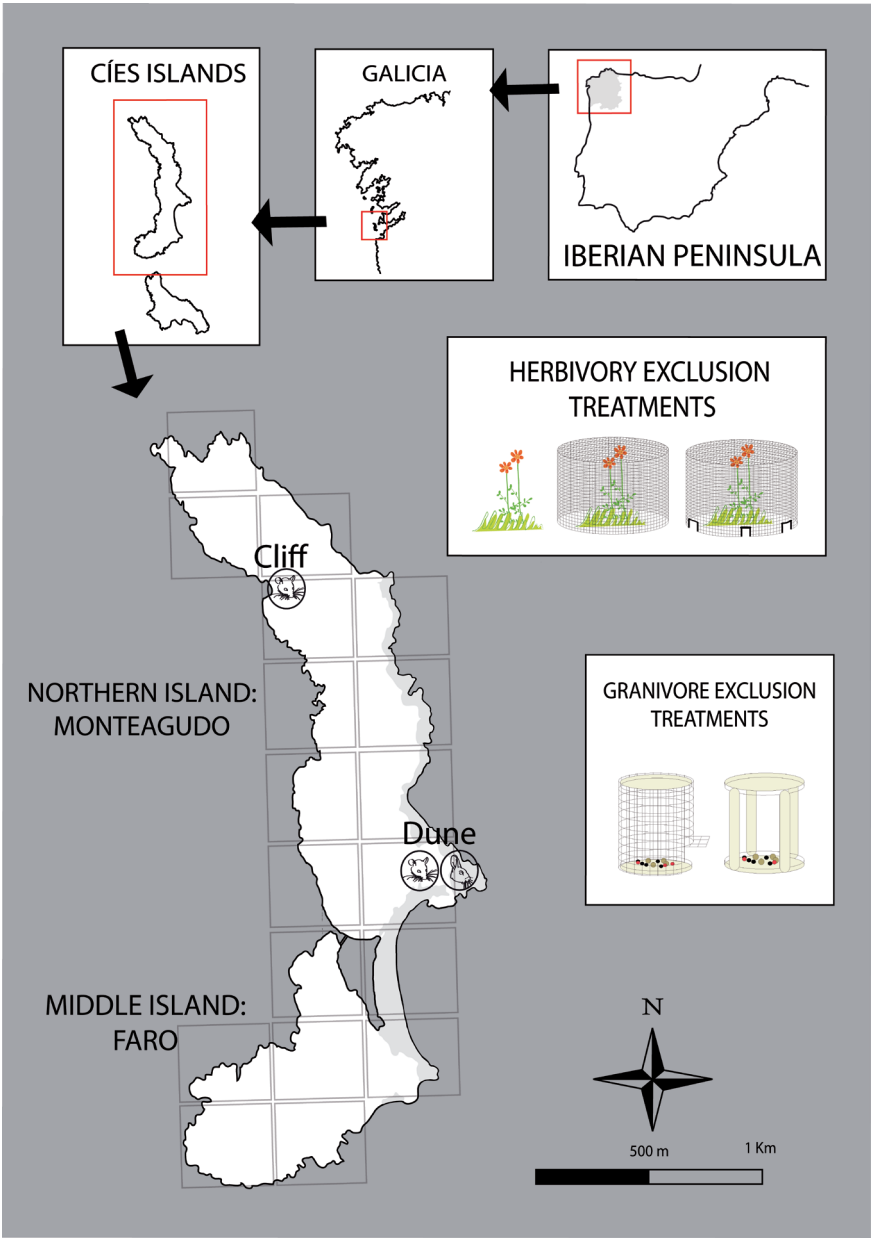


Figure 5.2. Study areas where the different demographic surveys and field experiments were undertaken. Herbivore exclusion treatments: from left to right: control (open), rat + rabbit exclusion, rabbit exclusion. Granivore exclusion treatments: from left to right, bird exclusion and control (open).

5.2 Materials and methods

5.2.1 Study site

The study took place at the joined Monteagudo (or Northern) and Faro (or Middle) Islands, two of the three continental Cíes Islands archipelago which belongs to the Atlantic Islands of Galicia National Park (NW Spain; 42°13'55.27''N, 8°54'11.56''W; Fig. 5.2). The two sum up 286.1 ha and are located 2.6 km offshore. Both islands have a rugged terrain (maximum height: 197 m) and an oceanic climate, with moderate precipitation (857 mm $year^{-1}$ on average) and temperature (annual average: 13.7ºC). Inland vegetation is dominated by native bushes (mainly gorse, *Ulex europaeus*) and small stands of several exotic species (*Eucalyptus globulus*, *Pinus pinaster*, *P. radiata* and *Acacia melanoxylon*). The coastal strip is dominated by halophilous shrubs, grasses and megaforbs (e.g. *Crithmum maritimum*, *Armeria pubigera*, *Festuca rubra*, *Daucus carota* and *Angelica pachycarpa*) in rocky areas and dune vegetation (including the shrubs *Corema album*, *Ulex europaeus, Rubus ulmifolius* and *Armeria pungens*) in sandy ones (Guitián & Guitián, 1990).

The native fauna includes one amphibian, eight reptile and 55 bird and five mammal species. Particular conservation importance is given to the local populations of fire salamander (*Salamandra salamandra*), eyed lizard (*Lacerta lepida*) and Iberian wall lizard (*Podarcis hispanica*), as well as the breeding colonies of European shag (*Phalacrocorax aristotelis*), yellow-legged seagull (*Larus michahellis*) and black-backed seagull (*Larus fuscus*). In addition, the islands host an invasion complex composed by a herbivore (European rabbit, *Oryctolagus cuniculus* L.), an omnivorous mesopredator (black rat, *Rattus rattus* L.) and two top predators (feral cat, *Felis catus* L. and American mink, *Neovison vison*, Schreber) – hereafter referred to as rabbit, rat, cat and mink, respectively. While the first sightings of American mink took place within the

last decade, following their accidental release from fur farms established in mainland Galicia during the 1970's (Munilla & Velando, 2010), the establishment of breeding populations of cat, rat and rabbit probably took place several decades or centuries ago. The invasion complex probably sustains trophic and competitive relationships that may result in mesopredator release (of rats depredated by cats and/or minks), hyperpredation (of seabirds depredated by minks and/or cats that use rabbits and/or rats as primary prey) and competitor release (between cats and mink).

The first sightings of American mink on the islands in 2008 has been associated to a sudden increase in the predation of breeding adults and chicks of European shag (*Phalacrocorax aristotelis aristotelis*), a seabird included in the Spanish National Catalog of Endangered Species and the Spanish Red Book of Birds. In fact, the long-term decline of the shag population over the last decades has been worsened by the presence of mink (Munilla & Velando 2010). Feral cats have been shown to impact the breeding colonies of shag populations on other islands (Domm & Messersmith 1990), but direct predation was never reported or observed on Cíes Islands; however, local shag experts believe that indirect impacts (e.g. nest and/or colony abandonment by breeding adults) are likely in areas where cats are abundant (A. Velando, pers. comm.).

5.2.2 Distribution and abundance of invasive mammals

In September-October 2009, the relative abundance of the four invasive mammals (rabbit, rat, cat and mink) was surveyed throughout both islands (Fig. 5.2). For this purpose, the area was divided in 18 UTM squares (500 x 500 m) and measured:

- Rabbit: the number of warrens, scratches and latrines (as well as the number of faecal pellets per latrine; Blanco & Villafuerte, 1993) along eight

100 m transects evenly distributed within each square. Whenever part of the square fell outside the islands, the number of transects was adjusted in proportion to the area of land included within it.

- Rat: the proportion of poison-free bait (Detex Blox®, 20 g per unit) consumed along three 100 m transects (10 baits per transect, at 10 m intervals) evenly distributed within each square. Consumption was estimated by recording the weight difference (to the nearest g) three days after setting the baits, and inspecting them for marks of rat incisives.

- Mink and cat: the number of scats along eight 100 m transects evenly distributed within each square (or a proportional number for squares with part of the surface on land), which coincided with those used to assess rabbit abundance. These transects were complemented with additional searching sessions, covering the area between transects (inasmuch as the terrain allowed human transit), primarily aimed at obtaining samples for diet analysis (see below).

5.2.3 Population dynamics of rat and rabbit

Abundance, density and demographic parameters of rat and rabbit were estimated by capture-mark-recapture using Tomahawk live-traps (Tomahawk Live Trap Co. ®). For rat, we used two trap grids set respectively in: (1) A cliff area covered by grass, close to a shag colony and situated in NW of Northern island (cliff hereafter; 42º14'34''N, 8º54'33''W), where 78 traps were set in a 6 x 13 grid spaced at 10 m intervals (Fig. 5.2). (2) A dune area situated SE of Middle island (dune hereafter; 42º13'41''N, 8º53'55''W), where 88 traps were set in an 8 x 11 grid spaced at 10 m intervals. In both cases, trapping grids were shaped to fit local topography. Trapping campaigns comprised 6 nights and were repeated, in both areas, twice a year (summer and autumn) between July 2008 and July 2010

– making a total of 6 campaigns for the cliff area and 4 in the dune area (where the trapping program was ended after October 2008 owing to the disturbance caused by control campaigns, based on the application of poisoned bait, applied by the National Park in adjacent areas). Captured individuals were weighed and measured (snout-cloaca and cloaca-tail length, initially measured to discard the presence of Brown rat, *Rattus norvegicus*) and marked by toe-clipping, after the sedation of the animal and subjected afterwards to customary disinfection.

For rabbit, we used a single trap grid, installed in the dune are, where 88 traps were set in an 8 x 11 grid spaced at 20 m intervals, overlapping with the rat grid. As for rat, trapping campaigns comprised 6 nights and were repeated twice a year from November 2008 to October 2009. Captured individuals were weighed, sexed and marked with numbered ear tags (LaQuick ®).

5.2.4 Diet of top predators (mink and cat)

All mink and cat feces collected in the extensive sampling (September/ October 2009) and in comparable surveys carried out on previous years (September-December 2008 and January–July 2009) were preserved in 90% alcohol and stored in a freezer until their subsequent dissection. All scats (*N*=30 and 84 for mink and cat, respectively) were shredded, washed and sieved (0.5 mm mesh size). All identifiable items (bones, feathers and hair) were assigned to the lowest taxonomic category possible, using reference collections. We determined the frequency and abundance of birds, fish, reptile or mammal remains. Birds were classified as passerines, birds of prey or seabirds, and mammals assigned to species when possible.

Based on these data, we calculated the frequency of occurrence (proportion of scats containing remains of a given prey) and the abundance per scat (minimum number of individuals per scat, taking into account the anatomy of the different

remains encountered) of each prey taxon. In addition, based on measured and published values of biomass per individual (Table 5.1), we estimated the contribution of each prey taxon to the predator's diet. Biomass calculations disregarded the smallest and/or least frequent species, as well as those we suspected to be a result of secondary ingestion (from the prey's stomach)

Species	Biomass (g)	Source
European rabbit *Oryctolagus cuniculus*	865	Own compiled data
Black rat *Rattus rattus*	137	Own compiled data
Yellow-legged seagull *Larus michahellis*	854	(1)
House mouse *Mus musculus*	20,75	(2)
Wood mouse *Apodemus sylvaticus*	25,5	(3)
Greater white-toothed shrew *Crocidura russula*	10,5	(4)
Passerines: house sparrow *Passer domesticus*	22	(5)

(1) Galarza *et al.* 2008, (2) Sans-Fuentes 2007, (3) Jubete 2007, (4) López-Fuster 2007, (5) Hume 2002

Table 5.1. Biomass values used for the calculation of the contribution of each prey taxon to the cat and American mink diets.

5.2.5 Impact of rabbit on native vegetation

The impact of rabbit and rat on native vegetation was assessed in the dune area. We focused our assessment on the vegetative growth and reproductive performance of two species of high conservation importance: the searose *Armeria pungens* (Link) Hoffmanns & Link (Plumbaginaceae) and the Portuguese crowberry *Corema album* (L.) D. Don (Empetraceae). The population of *C. album* at Cíes Islands represents the northernmost extreme of the species' distribution range and is the second-largest population of the Galician region (Blanco-Dios 2008). *A. pungens* presents a disjoint distribution in the Iberian Peninsula, with Cíes Islands hosting the only population in Northern Spain, separated by >400 km from all other populations in the Southern Spain and Portugal (Piñeiro *et al*.

2007).

Three treatments were randomly assigned to 56 haphazardly-selected searose and 120 crowberry individuals (Fig. 5.2): (a) Control treatment, in which the plants were accessible to all herbivores (*N*=21 and 38 for searose and crowberry, respectively); (b) Rabbit exclosures, in which each plant was covered by a cylinder of wire mesh (2 cm mesh size) with two small holes (6 x 6 cm) on the base to allow access of rat but not rabbit (*N*=20 and 37 for searose and crowberry, respectively); (c) Rat + rabbit exclosures, in which each plant was covered by a cylinder of wire mesh (2 cm mesh size) preventing the access of both rat and rabbit - i.e. allowing only insect herbivory (*N*=19 and 45 for searose and crowberry, respectively).

Control plants were marked and exclosures installed in July 2008, following initial measurements of size (height, major axis and minor axis), reproductive effort for searose (number of inflorescences per plant) and reproductive success for crowberry (number of fruits per plant) in all selected individuals. The same variables were measured again in July 2009 and 2010. Plant size was estimated as rosette volume, assuming a hemiellipsoid shape so that V= (4Π /3*a/2*b/2*h)/2, where h=height, a= major axis and b= minor axis.

In the same area, we estimated consumption by native (passerine birds) and invasive (rat) seed predators in 180 Petri dishes directly placed on the ground, which were assigned to two different treatments (*N*=90 each) using a paired design stratified under three microhabitat types (bare sand, grassland and under shrub, the latter referring to crowberry shrubs): (a) Control treatment, referring to open dishes allowing access to all granivores (but covered, at 10 cm height, with another Petri dish to protect seeds from the impact of rain drops); (b) Bird exclusions, referring to dishes covered by a wire mesh cylinder (2 cm mesh size) with two small (6 x 6 cm) holes on the base, covered by a small cornice, to

allow access by rats but not passerine birds (Fig. 5.2).

In both treatments, seed removal by insects was prevented by the application of insect-trapping glue (TemoBi ® de Kollant) and ant-specific insecticide (K.B. ®) to the inner perimeter of the Petri dish. Each tray contained 69 seeds of five different species present in the area (crowberry, *Cytisus insularis*, *Osyris alba*, *Rubus ulmifolius* and *Tamus communis*; *N*=16 seeds for each species, except for *O. alba* in which *N*=5). Trays with seeds were set in December 2008, and the number of seeds recorded regularly at 20 to 40-day intervals (depending on the accessibility to the island) for 124 days (i.e. until April 2009).

5.2.6 Statistical analysis

Distribution and abundance of invasive mammals

Data from the extensive survey were used to calculate relative abundance indices for each invasive species, as follows:

- Rabbit: the three variables registered (the number of scratches, latrines, and faecal pellets per transect; no warrens were found on the transects) were subjected to principal component analysis. The first principal component, which explained 72.5% of the total variance and showed strong correlations with the three original variables (*r*=0.69-0.91), was used as the relative abundance index.

- Rat: the proportion of bait consumed (as % of the original weight) was averaged among all transects within each 500 x 500 m square and used as the relative abundance index.

- Cat: the proportion of scats found in a given 500 x 500 m square (i.e. the average number of scats per transect within that square divided by the average number of scats per transect across the whole island) was used

as the relative abundance index.

- Mink: owing to the low number of mink scats found, the presence/absence of mink scats was used as surrogate of mink presence/absence in each square.

Spatial relationship among the four invasive species was evaluated using an association index based on the SADIE software (Perry 1995, 1998). First, SADIE computes an index of spatial aggregation or clustering of each variable (I_a, where I_a=1 for random spatial distribution, I_a<1 for regular distribution and I_a>1 for aggregated distribution). Second, SADIE computes a pairwise association index for each pair of variables, measuring in our case whether high (or low) abundance squares of one species are associated with high (or low) abundance squares of the other (Perry *&* Dixon 2002). The association statistic (X) ranges from 1 (total association) to -1 (total dissociation). X>0 indicates association between both variables, X<0 indicates dissociation between both variables and X=0 indicates a random relationship between both variables. In both cases, associated p-values 0.025 indicate significant aggregation for *P* <0.025 and significant regularity or dissociation for *P* >0.975.

Population dynamics of rat and rabbit

Capture-mark-recapture data were analyzed using MARK 6.0 (White *&* Burnham 1999). Different models were used to meet the data requirements of the two different rat populations' data sets. In the cliff population, robust models with Huggins parameterization and rat weight as a covariate provided the best fit (Huggins 1989; Alho 1990; Huggins 1991). Temporal variability and capture response were considered. In the dune population, lack of captures during the April 2009 campaign (caused by the application of poisoned baits in the vicinity) prevented the use of robust models to the complete data set (three campaigns).

Symbol	Parameter	Units	Values used for reference and control scenarios
r_R	Growth rate of rabbit population	Ind.* ind.$^{-1}$ *year^{-1}	1.46
r_B	Growth rate of rat population	Ind.* ind.$^{-1}$ *year^{-1}	3
r_M	Growth rate of mink population	Ind.* ind.$^{-1}$ *year^{-1}	0.6
r_C	Growth rate of cat population	Ind.* ind.$^{-1}$ *year^{-1}	0.25
K_R	Carrying capacity of rabbit population	Ind.	1188
K_B	Carrying capacity of rat population	Ind.	35434.5
γ_{RM}	Predation rate of minks on rabbits	Ind.*ind.$^{-1}$	64
γ_{BM}	Predation rate of minks on rats	Ind.*ind.$^{-1}$	400
γ_{OM}	Predation rate of minks on other native prey	Ind.*ind.$^{-1}$	2600
γ_{RC}	Predation rate of cat on rabbit	Ind.*ind.$^{-1}$	80
γ_{BC}	Predation rate of cat on rat	Ind.*ind.$^{-1}$	505
γ_{OC}	Predation rate of cat on other native prey	Ind.*ind.$^{-1}$	3300
η_{RM}	Preference of minks for rabbits	Dimensionless	8
η_{BM}	Preference of minks for rats	Dimensionless	3
η_{OM}	Preference of minks for other native prey	Dimensionless	1
η_{RC}	Preference of cat for rabbit	Dimensionless	4
η_{BC}	Preference of cat for rat	Dimensionless	4
η_{OC}	Preference of cat for other native prey	Dimensionless	1
μ_M	Mink migration rate	Ind. *year^{-1}	2
τ_R	Mortality caused by rabbit control program	Ind .*ind.$^{-1}$ *year^{-1}	0 to 0.9 at 0.1 intervals
τ_B	Mortality caused by rat control program	Ind .*ind.$^{-1}$ *year^{-1}	0 to 0.9 at 0.1 intervals
τ_M	Mortality caused by mink control program	Ind .*ind.$^{-1}$ *year^{-1}	0 to 0.9 at 0.1 intervals
	Initial conditions		
R_0	Rabbit population size	Individuals	800
B_0	Rat population size	Individuals	24000
M_0	Mink population size	Individuals	0
C_0	Cat population size	Individuals	20

Table 5.2. Parameters of the demographic model (definition, units and values used in the simulations).

Hence, we fitted closed population models separately to the first (November 2008) and last (October 2009) campaigns (Otis *et al*. 1978). In both populations, density was estimated by dividing the estimated abundance by the corrected area of the trap grid. The correction involved adding to the total area of the trap grid a boundary strip which width was half of the mean distance covered by the rats on each campaign (Otis *et al*. 1978).

The low capturability of rabbit in all campaigns prevented the use of statistical analyses. Hence, we only report the number of captures per campaign (which corresponds also to captures per unit effort, since trapping effort was constant among campaigns).

Impact of rabbit and rat on native vegetation

The effects of herbivore-exclusion treatments on plant size (rosette volume) and reproduction (inflorescence production for searose, fruit production for crowberry) were assessed using repeated measures analyses of plant size, separately for searose and crowberry. Models included treatment as fixed effect, time (year) as within-subject effect and individual plant as subject. For all variables except for crowberry reproduction we used linear mixed models (MIXED procedure, SAS ® v.9 SAS Institute 2000). Log-transformation was used for both plants volume, to achieve residual's normality and homoscedasticity. For crowberry reproduction, we used the GLIMMIX procedure in SAS with a log-normal error distribution and an identity link.

The effect of granivore-exclusion treatments on two different variables describing seed removal (seed survival at the end of the experiment and the life expectancy of consumed seeds, i.e. the number of days from the beginning of the experiment to consumption, for each individual seed) was assessed using repeated measures analysis (GLIMMIX procedure in SAS). Models included

microhabitat and species as fixed factors, tray as a random factor (to account for the dependence of seed predation events taken place on seeds offered on the same tray), a binary error distribution with logit link for seed survival, and a log-normal error distribution with identity link for seed life expectancy. A few trays became covered by sand, soaked in rain or broken during the experiment and had to be excluded from the analysis, leaving a final sample size of 141 trays.

Demographic model

Based on the results of the previous sections and on parameters reviewed from the literature (Table 5.2), we built a demographic model to analyze the dynamics of the invasion complex and its impact on a native species of conservation priority (the European shag). The impact of exotic herbivores on the two plant species of conservation considered was not included in the model, since its existence was not supported by our empirical data (see Results). The purpose of the model was double: (i) to evaluate the existence of counterintuitive effects (hyperpredation, mesopredator release and/or competitor release) in the mink-cat-rabbit-rat-shag system and (ii) to compare the effect of different control strategies on the invasion complex and the shag population. The five-species model was based on the equations developed by Courchamp (Courchamp, Langlais & Sugihara 1999a, 1999b, 2000; Caut *et al*. 2007; Russell *et al*. 2009) and incorporated the effect of selection among prey species by the predator (Russell *et al*. 2009). The terms describing the population dynamics of the prey (rabbit *R*) and mesopredator (black rat *B*) species are based on logistic equations, and include a term describing the predation of rabbit, rat and other native prey (*O*) by either mink (*M*) or cat (*C*) that incorporates the predation rate of mink and cat (γ_M and γ_C) and their relative preference for each prey species (η_M and η_C; see Table 5.2 for a description of the meaning, units and values of all parameters

used in the equations shown below):

$$\frac{\partial B}{\partial t} = r_B B\left(\frac{1-B}{K_B}\right) - V\gamma_{BM}\left(\frac{\eta_{BM}B}{\eta_{BM}B+\eta_{RM}R+\eta_{OM}O}\right) - G\gamma_{BC}\left(\frac{\eta_{BC}B}{\eta_{BC}B+\eta_{RC}R+\eta_{OC}O}\right) - \tau_B B$$

$$\frac{\partial R}{\partial t} = r_R R\left(\frac{1-R}{K_R}\right) - V\gamma_{RM}\left(\frac{\eta_{RM}R}{\eta_{BM}B+\eta_{RM}R+\eta_{OM}O}\right) - G\gamma_{RC}\left(\frac{\eta_{RC}R}{\eta_{BC}B+\eta_{RC}R+\eta_{OC}O}\right) - \tau_R R$$

The terms describing the population dynamics of both predator (mink and cat) species are based on logistic equations, in which the carrying capacity is determined by the abundance of the different prey and the predation rates exerted by the predator specific on each of them (i.e. the number of prey individuals consumed per day):

$$\frac{\partial M}{\partial t} = r_M M\left(\frac{1-M}{\frac{B}{\gamma_{BM}}+\frac{R}{\gamma_{RM}}+\frac{O}{\gamma_{OM}}}\right) + \mu_M - \tau_M M$$

$$\frac{\partial C}{\partial t} = r_C C\left(\frac{1-C}{\frac{B}{\gamma_{BC}}+\frac{R}{\gamma_{RC}}+\frac{O}{\gamma_{OC}}}\right) - \tau_C C$$

These terms include also a parameter describing the availability of a third trophic resource (other native prey, *O*, such as fish and small birds) that did not depend on predator abundance, which ensures model stability whenever prey species go extinct; as well as a parameter describing the effect of control programs (τ), expressed in terms of *per capita* mortality to reflect the decrease in encounter (thus capture or poisoning) rate at decreasing abundances of the target species. Finally, the term for mink includes also a parameter describing the migration rate of mink into the island (μ_M).

As a surrogate of the impact of the invasion complex on native species,

we chose the effect on European shag. We therefore included in the model a simple description of shag population dynamics based on the age structure (four age classes: chicks, 1-year juveniles, 2-year juveniles and adults), transition probabilities (0.42, 0.7 and 0.72, respectively) and reproductive rates (0.36 and 1.45 for of 2-year juveniles and adults, respectively) published by Munilla & Velando (2010). The impact of mink on shag included both predation on reproductive individuals (adults and 2nd year juveniles, at a rate of 0.0025 shags/mink/year) and nest abandonment (which increased linearly with mink abundance until saturating at 90% abandonment for a population of 30 minks) – in agreement with field data showing that, in 2009, a population of at least 26 minks (subsequently captured during the 2009-10 control program; Romero R., pers. comm.) caused the direct death of 5% shag adults and the abandonment of approx. 90% shag nests (Munilla & Velando 2010). The impact of rat on shag included chick predation ($1.9*10^{-6}$ chicks/rat/year, calculated to obtain a predation of 5% chicks for a total population of 26,000 rats).

We run a number of simulations that evaluated the outcome of different strategies for the control on the invasive species, as follows: (1) individual control of each invasive species (4 simulations), (2) simultaneous control both top predators (1 simulation), (3) simultaneous control of both prey species (herbivore and mesopredator; 1 simulation), and (4) simultaneous control of mink and prey (each prey separately plus both prey simultaneously; 3 simulations) (9 simulations). For each of these strategies, we simulated control efforts of variable intensity (ranging from 0 to 90% target-species mortality) and evaluated their impact on the different species of the invasion complex and the shag population.

5.3 Results

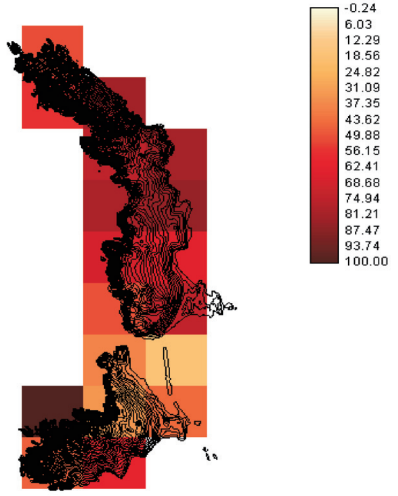
5.3.1 Distribution and abundance of invasive mammals

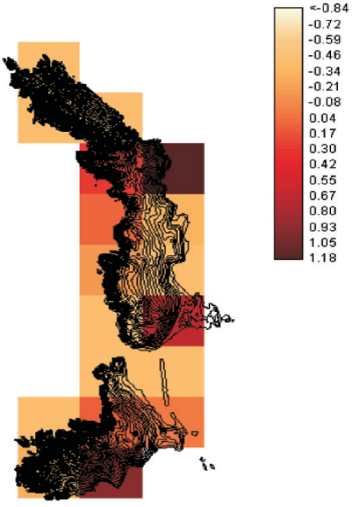
Both prey species (rabbit and rat) were widespread across both islands, while cat and mink showed a more scattered distribution (Fig.5.3). None of the four invasive species showed a significant departure from a random spatial distribution (I_a=0.78 to 1.31; Table 5.3). Similarly, none of the pairwise analyses indicated significant spatial association or dissociation between invasive species (Fig.5.3, Table 5.4), although rabbit and mink showed a marginally-significant positive association.

5.3.2 Population dynamics of rat and rabbit

Rat: Data from the cliff population indicated that apparent survival varied among years and between seasons, ranging from 0.71 (winter 2009) to 0.99 (summer 2008). Rat mortality was concentrated in winter (mean survival = 0.72 and 0.99 in winter and summer, respectively). Rat abundance decreased abruptly from 2008 to 2009-2010 (Fig. 5.4), coinciding with a sharp increase of European shag depredation by mink (Munilla & Velando 2010). Rat density was considerably lower in the dune than in the cliff population (Fig. 5.4), although data from the former should be considered with caution (see Methods), owing to the effect of poisoned-bait application in spring 2009 (no captures during the six nights of sampling).

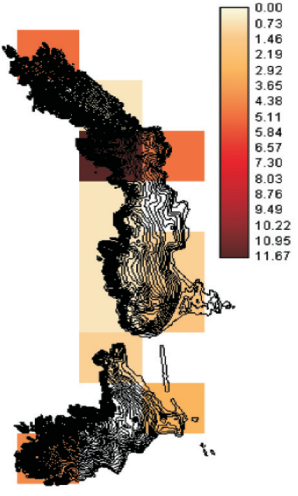
Rabbit: In the dune population, relative abundance (estimated from the number of captures per unit effort) was similar for both sexes and increased from autumn 2008 to autumn 2009, with an intermediate decrease in spring of 2009 probably related to the application of poisoned bait (as above; Fig. 5.4).

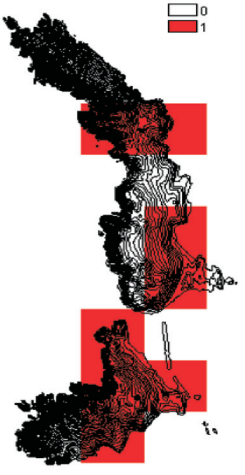




Rat

Rabbit





Cat

Mink

Figure 5.3. Spatial distribution and relative abundance of four invasive mammal species on Cíes Islands. Values indicate relative abundance indices for cat, rabbit and rat, and presence-absence for mink (see text for details).

Species	I_a	*P*
Rat	1.3100	0.1500
Rabbit	0.7780	0.7654
Cat	1.1900	0.2846
Mink	1.0420	0.3390

Table 5.3. Aggregation index and its associated probability for the four study species. I_t=1 indicates random distribution, I_t>1 spatial aggregation and I_t<1 regularity. None of the species showed significant aggregation or regularity (*P* <0.025 and *P* >0.975, respectively).

Association	I_t	*P*
Rat-Rabbit	0.1499	0.3151
Rat-Cat	0.2819	0.1831
Rat-Mink	-0.0351	0.5527
Rabbit-Cat	0.3401	0.1673
Rabbit-Mink	0.6058	0.0329
Cat-Mink	0.0094	0.4808

Table 5.4. Inter-specific association index and its associated probability for the four study species. I_t=0 indicates random distribution, I_t>0 spatial association, I_t<0 dissociation. None of the species showed significant aggregation or dissociation (*P* <0,025 and *P* >0,975, respectively).

		Feral cat		American mink	
Prey		# prey	% biomass	# prey	% biomass
Mammals					
	Oryctolagus cuniculus	12	31.00	3	25.95
	Rattus rattus	136	55.64	8	10.96
	Mus musculus	92	5.71	16	3.32
	Crocidura russula	19			
	Unknown rodent	1			
Birds					
	Seabirds	3	7.65	7	59.77
	Passerines	1		2	
	Raptors			1	
	Unknows birds	1		5	
Reptiles				1	
Fishes		4*			
Crustaceans		1*			
Molluscs				5	
Insects		10		3	
Seeds		12*		1	
Unknown prey		7		12	

Table 5.5. Diet composition of feral cat and American mink on Cíes Islands, as estimated from the analysis of collected scats (*N*=84 and 30 for cat and mink, respectively). # prey: estimated number of prey individuals found in the complete sample of scats. % biomass: proportion of biomass of the different prey, estimated from the number of individuals and body mass of the different prey taxa. Asterisk indicate taxa representing <1 % of biomass that are probably scavenged from human waste (or, in the case of seeds, the result of secondary ingestion).

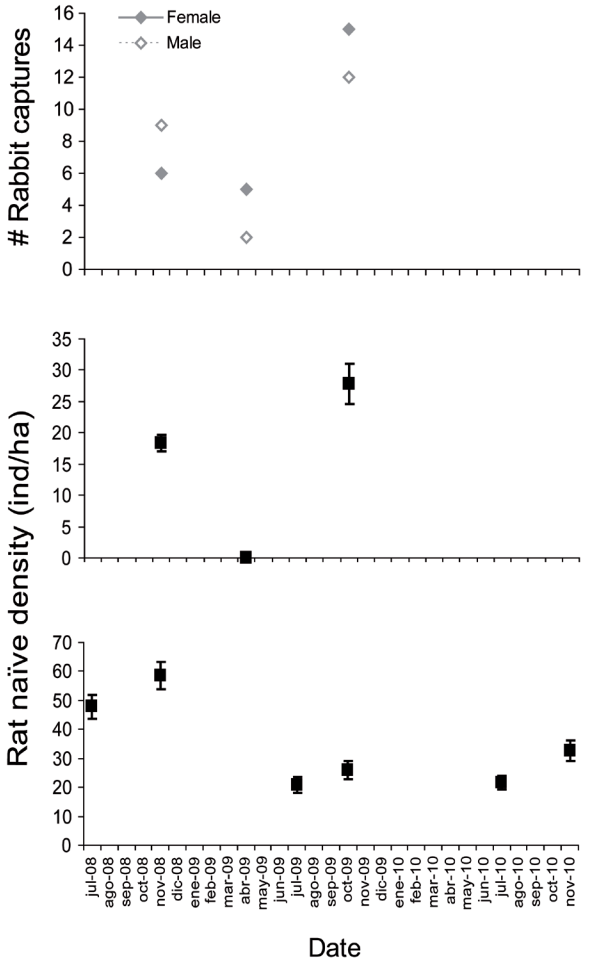


Figure 5.4. Results of capture-mark-recapture of invasive rabbit and rat on Cíes Islands. Upper panel: number of rabbit captures per unit effort (6 trapping nights with 88 traps per campaign) in the dune area. Middle and lower panel: estimated rat density (individuals per ha), based on 6 trapping nights (in both areas) with 88 and 78 traps per campaign, in the dune and cliff areas respectively.

5.3.3 Diet of top predators (mink and cat)

Data on frequency of occurrence (proportion of scats with prey remains) and number of prey items per scat were virtually identical; hence, we report here only on the latter. While the diet of both top predators (mink and cat) was largely based on invasive mammals (rabbit and rat), there were considerable differences

between them. Regarding the number of prey items, cat captured primarily rodents (46% of rat and 31% of house mouse, *Mus musculus*) while mink's diet was more diverse (Table 5.5). However, when expressed as biomass, cat diet was primarily based on invasive mammals (56% rat and 31% rabbit *vs*. 8% seabirds) while mink diet relied strongly on seabirds (60% seabirds *vs*. 26% rabbit and 11% rat).

5.3.4 Impact of rabbit and rat on native vegetation

Herbivore-exclusion treatments had significant effects on neither plant size (time*treatment interaction: $F(4,93)=0.18$, $P>0.10$ and $F(4,201)=0.02$, $P>0.10$, for searose and crowberry respectively) nor reproduction (time*treatment interaction: $F(4,95)=0.79$, $P>0.1$ for searose inflorescence production, $F(3,16)=0,31$, $P>0.1$ for crowberry fruit production; Table 5.6).

In contrast, rats caused considerably more seed predation than native species. The exclusion of native birds and insects reduced seed predation (treatment effect on seed survival: $F(1,61)=446.37$, $P<0.0001$) by only one third (from 96 to 60% of seed removed). Treatment effects varied, however, among microhabitats and species (treatment*microhabitat*species interaction:

Table 5.6. Results of Linear Mixed Model and Generalized Linear Mixed Model for the effect of herbivore exclusion treatments on growth and reproduction of searose (*Armeria pungens*) and Portuguese crowberry (*Corema album*).

	Armeria pungens						*Corema album*					
	Growth			Inflorescence production			Growth			Fruit production		
	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F	d.f.	F-value	Pr> F
Treatment	2;53	6.46	**0.0031**	2;53	3.27	**0.0456**	2;117	1.76	0.1773	3;28	1.03	0.3957
Year	2;93	3.38	**0.0382**	2;95	10.88	**<0.0001**	2;201	7.43	**0.0008**	1;16	0.13	0.7252
Treatment*Year	4;93	0.18	0.9488	4;95	0.79	0.5332	4;201	0.02	0.9988	3;16	0.31	0.8153

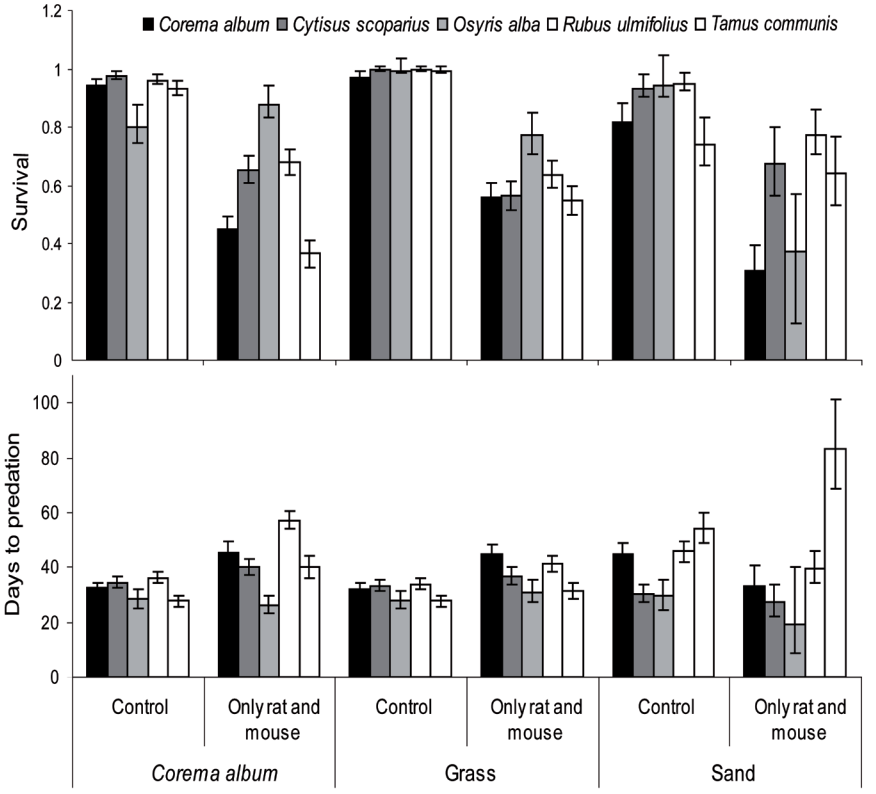


Figure 5.5. Effect of rat on the survival (upper panel) and life expectancy (lower panel) of seeds of five native plant species in the Figueiras-Muxieiro dune, Cíes Islands. Control trays (open) allowed access to all granivores, while bird exclosures excluded native passerine birds while allowing access by rats.

F(8,189)=8.57, *P* <0.0001; Fig. 5.5), being much smaller for larger seeds (e.g. non-significant contrasts *for O. alba* under shrubs and for *T. communis* on bare sand, *P* >0.10; Table 5.7, Fig. 5.5) for which rats caused most predation. Moreover, seed predation took only slightly longer in the bird-exclosures than in the open trays (35.4 *vs*. 33. 0 days; treatment effect: F(1,57)=11.70, *P* <0.01) and varied much less (though still significantly: F(8,182) =6.20, *P* <0.0001 for treatment*microhabitat*species) among species and microhabitats (Table 5.8; Fig. 5.5).

	Fixed effects Type III Tests			Tests of Effect Slices for Microhabitat*Treatment*Specie Sliced By Species			
	d.f.	F-value	Pr> F	Species	d.f.	F-value	Pr> F
Treatment	1;61	446.37	**<0.0001**	*Corema album*	5;189	72.61	**<0.0001**
Microabitat	2;76	27.79	**<0.0001**	*Cytisus scoparius*	5;189	40.62	**<0.0001**
Species	4;269	19.12	**<0.0001**	*Osyris alba*	5;189	7.35	**<0.0001**
Treat.*Microhab.	2;61	21.05	**<0.0001**	*Rubus ulmifolius*	5;189	37.09	**<0.0001**
Treat.*Species	4;189	1.46	0.2165	*Tamus communis*	5;189	63.47	**<0.0001**
Microhab .* Species	8;269	2.27	**0.0229**				
Treat.* Microhab .* Species	8;189	8.57	**<0.0001**				

Tests of Effect Slices for Microhabitat *Treatment*Species Sliced By Microhabitat *Species

Microhabitat	Species	d.f.	F-value	Pr > F
Corema album	*Corema album*	1;189	190.59	**<0.0001**
Corema album	*Cytisus scoparius*	1;189	92.79	**<0.0001**
Corema album	*Osyris alba*	1;189	2.84	**0.0937**
Corema album	*Rubus ulmifolius*	1;189	88.06	**<0.0001**
Corema album	*Tamus communis*	1;189	229.63	**<0.0001**
Grass	*Corema album*	1;189	111.23	**<0.0001**
Grass	*Cytisus scoparius*	1;189	50.72	**<0.0001**
Grass	*Osyris alba*	1;189	12.89	**0.0004**
Grass	*Rubus ulmifolius*	1;189	43.39	**<0.0001**
Grass	*Tamus communis*	1;189	74.82	**<0.0001**
Sand	*Corema album*	1;189	58.05	**<0.0001**
Sand	*Cytisus scoparius*	1;189	21.89	**<0.0001**
Sand	*Osyris alba*	1;189	17.76	**<0.0001**
Sand	*Rubus ulmifolius*	1;189	19.10	**<0.0001**
Sand	*Tamus communis*	1;189	1.95	**0.1639**

Table 5.7. Results of Generalized Linear Mixed Model for the effect of granivore exclusion treatments on the survival of seeds from six different plant species.

5.3.5 Demographic model

In the reference simulation (current conditions without any control actions), mink and cat populations increased, causing the shag population to decrease until extinction in less than 20 years (Appendix 1.A). Rat and rabbit populations decreased following an initial peak, but maintained moderately high abundances that support high numbers of both top predators. Control programs targeting single species may result in eradication of some species (notably cat and rabbit) at moderate effectiveness (e.g. >30% mortality for cat) and with very limited

effects on other components of the invasion complex (owing to the availability of alternative prey for predators and to the effect of alternative predators for prey). Mink control had considerable positive effects on the shag population (Appendix 1.B), which increased its persistence from <20 to >50 years, though still showing a strong decrease over time.

Multiple interactions within the invasion complex made counterintuitive effects moderate or absent. Mesopredator release was moderate in response to cat or mink eradication (e.g. 60% increase in rat abundance following 75% mink control; Appendix 1.B) and fairly strong when both predators were controlled (e.g. 150% increase in rat abundance following 75% mink + 75% cat control; Appendix 1.C). Under the model's assumption of a moderate effect of rat on shag reproduction, however, mesopredator release did not have strong effects in shag

Table 5.8. General Linear Mixed Model results for the effect of herbivore exclosures on seed life expectancy.

	Fixed effects Type III Tests			Tests of Effect Slices for Habitat*Treatment*Species Sliced By Species			
	d.f.	F-value	Pr> F	Species	d.f.	F-value	Pr> F
Treatment	1;57	11.70	**0.0012**	*Corema album*	5;182	16.15	**<0.0001**
Habitat	2;74	9.76	**0.0002**	*Cytisus scoparius*	5;182	5.55	**<0.0001**
Species	4;267	29.10	**<0.0001**	*Osyris alba*	5;182	0.99	0.4234
Treat.*Hab.	2;57	6.85	**0.0022**	*Rubus ulmifolius*	5;182	38.71	**<0.0001**
Treat.*Species	4;182	6.64	**<0.0001**	*Tamus communis*	5;182	45.08	**<0.0001**
Hab.* Species	8;267	25.83	**<0.0001**				
Treat.*Hab.* Species	8;182	6.20	**<0.0001**				

Tests of Effect Slices for Habitat*Treatment*Species Sliced By Habitat*Species

Habitat	Species	d.f.	F-value	Pr > F
Corema album	*Corema album*	1;182	25.21	**<0.0001**
Corema album	*Cytisus scoparius*	1;182	0.91	0.3420
Corema album	*Osyris alba*	1;182	0.02	0.8912
Corema album	*Rubus ulmifolius*	1;182	109.83	**<0.0001**
Corema album	*Tamus communis*	1;182	21.48	**<0.0001**
Grass	*Corema album*	1;182	40.31	**<0.0001**
Grass	*Cytisus scoparius*	1;182	1.74	0.1882
Grass	*Osyris alba*	1;182	1.45	0.2296
Grass	*Rubus ulmifolius*	1;182	19.73	**<0.0001**
Grass	*Tamus communis*	1;182	3.80	0.0529
Sand	*Corema album*	1;182	9.45	**0.0024**
Sand	*Cytisus scoparius*	1;182	0.81	0.3707
Sand	*Osyris alba*	1;182	1.93	0.1666
Sand	*Rubus ulmifolius*	1;182	2.48	0.1168
Sand	*Tamus communis*	1;182	12.66	**0.0005**

abundance (Appendix 1B-C.).

Competitor release between top predators was also evident in the scenarios where either mink or cat was targeted by control programs. In particular, mink control resulted in a 38% increase in cat abundance; the increase in cat abundance, however, did not suffice to compensate the effect of decreased mink abundance on both prey – which showed a moderate increase in abundance (Appendix 1.B).

Hyperpredation effects were also very small following single-species control programs (i.e. on rat or rabbit), owing to the availability of alternative prey for both top predators. Simultaneous control of both invasive prey species, in contrast, evidenced the existence of strong hyperpredation effects within the invasion complex. Control of rabbit and rat resulted in strong decreases in the abundance of both top predators – although, in the absence of simultaneous control of top predators, it only caused a small delay in the decline of the shag population (Appendix 1.F). Combined control of mink and rat increased the positive effects on mink control on the shag population, particularly if rabbit was also targeted: mink + rat and mink + rat + rabbit control (always with a 75% efficiency) resulted in the persistence of 60% and 90% of the original population after 50 years, respectively (Appendix 1.E-G). In contrast, combined control of mink + rabbit did not result in any improvement for shag population dynamics, as compared with single-species control of mink (Appendix 1.D).

5.4 Discussion

The different species of the invasion complex on Cíes Islands engaged in a number of interactions that resulted in complex responses to (simulated) management actions. In particular, both top predators (mink and cat) obtained a significant part of their diet from invasive prey (rabbit and rat), while only

mink based a considerable part of its diet on native seabirds. Moreover, the strong decrease of rat following the first sightings of mink on the islands also suggested that strong effects on prey populations can be expected even at low abundances of top predators. These data are compatible with the three potential counterintuitive responses: mesopredator release (of rat following mink and/or cat control), hyperpredation (apparent competition between native prey, shag, and invasive prey, rat and rabbit, mediated by mink predation) and/or competitor release (between mink and cat, since they share their main prey). Demographic modeling confirmed all these effects, albeit two important differences with those reported for simpler invasion complexes (i.e. with only two invasive species) were detected: (i) strong responses only appeared after multi-species control programs (both predators for mesopredator release, mink + rat + rabbit for hyperpredation), i.e. single-species control programs did not result in strong counterintuitive effects, and (ii) only one of the three effects (hyperpredation) had strong implications for the conservation of native prey (shag). From an applied point of view, simultaneous control of mink and invasive prey (rat and rabbit) represents the best option for shag conservation, although monitoring should be established to evaluate potential effects of cat on shag (undetected to date).

Interactions among invasive species were not affected by (or reflected in) their spatial distribution: while some species showed strong variation in abundance at the scale assessed (500 x 500 m squares), there was neither significant patterning at larger scales nor significant association or dissociation between species. This is not surprising, given the relatively small size of the studied islands, the demonstrated ability of both invasive prey (rat and rabitt) to achieve high abundances in insular systems, and the capacity that both top predators have for exploiting relatively large territories (251200 ha in Reunion Island for cat, 217900 ha. in Lewis & Harris for mink; Faulquier *et al*. 2009 and Clode & Macdonald

2002) – hence, to homogenize prey abundance at such scale. This, together with the lack of significant effects of rats and rabbits on the two native plants of conservation interests, suggested that a simple demographic model centered on the impact of the invasion complex on endangered seabird (shag) could provide a reasonable evaluation of the various management options.

The high dependence of invasive predators on rat and rabbit was coherent with the low availability of native prey (seabirds are only available during the breeding season) and the high density of invasive prey - particularly rat, whose 2008 densities (48-59 and 18 ind ha^{-1} dune in the cliff and dune areas, respectively) were in the upper range of those usually reported from invaded islands (0.5 to 6.5 ind ha^{-1} at New Zealand or 0.2 to 18.9 ind ha^{-1} at Galápagos; Innes *et al.* 2010 and Clark 1981 respectively). Despite these high densities, the rapid decline of rat density following the first sightings of mink on the island (from 50-60 to 20-30 ind ha^{-1} in 2008 and 2009-10, respectively, in the cliff area; Fig.5.4) suggests the build-up of moderate densities of top predators (26 mink captured during the control program that took place in 2009-10) has the potential to induce rapid changes in the abundance of invasive prey. (This trend cannot be assessed in the dune area because, following the drop in density caused by the application of poisoned bait, the increase in rat density and rabbit abundance probably reflects a population rebound related to an increased availability of resources).

Given their high abundance (before the arrival of mink), the absence of significant effects of both native herbivores (rabbit and rat) on the two native species of conservation interest (searose and crowberry) was surprising, and contradicted previous results on Atlantic (Latorre, chapter 4 in this thesis) and Mediterranean (Latorre, Larrinaga & Santamaría 2013) continental islands. It is important to note, however, that our exclusion treatments took place in the dune area; hence, it is possible that the transitory impact of the rat-control campaign

on rat and rabbit abundance introduced a negative bias in our result. The simultaneous measurements of seed predation by rats, which doubled those of native granivores, suggest however that strong effects show up even under such conditions. Although, based on the lack of evidence in our data, the impact of rat and rabbit on native vegetation was not included in the final model. Providing a more detailed assessment of such effects represent a clear priority for future monitoring programs on the island.

Feral cat showed also a surprisingly low impact on native fauna, as evidenced by the small proportion of native prey in its diet – while the impact of mink was much larger. As expected for two generalist predators, and similar to that reported for sympatric cats and mustelids in continental areas (Murphy *et al*. 2004), they showed a considerable dietary overlap – which increased the potential for competitor release effects but buffered the existence of hyperpredation and mesopredator release effects in response to single-species control programs (see below). Nevertheless, while cat diet was based on a low diversity of prey and relied strongly on invasive prey (rat and rabbit), mink consumed a more diverse array of prey (typical of semi-aquatic animals, Delibes *et al*. 2004) and consumed a high proportion of seabirds (60% of biomass consumption). Seabird predation was reflected in the strong predation rates reported on local shag colonies: in 2009, mink preyed on 5% of nesting adults and caused the abandonment of 95% shag nests (Munilla & Velando 2010).

Demographic modeling confirmed that the dependence of top predators on both invasive prey buffered the counterintuitive effects of single-species control but caused them to emerge in response to multi-species control. As a consequence, mesopredator release effects were only predicted following the simultaneous control of mink and cat, and hyperpredation effects were only evidenced by the simultaneous control of mink + rat or mink + rat + rabbit. Only one of the three

effects (hyperpredation) had strong implications for the conservation of native prey (shag). More importantly, our model predicted mink control (as currently undertaken) to provide a fairly limited improvement in shag conservation; and only options including the additional control of either one (rat) or both invasive prey (rat and rabbit) would add significant improvement over single-species mink control.

Although the demographic model provides a useful tool for *ex ante* evaluation of potential control programs, it is important to stress its numerous limitations – arising from both its simplicity (i.e. the simplifying assumptions on which the demographic equations are based) and its complexity (i.e. the relatively high number of parameters, which multiply the uncertainty associated to the model's output). Model outputs should therefore be tested against the results of monitoring data associated to any control program undertaken, and the conclusions revised accordingly. Amongst the assumptions to be evaluated, one must include those regarding processes excluded from the model – in particular, the lack of detectable effects of cat on shag. Hence, even if cat is tentatively not considered of major conservation concern, it is important to dedicate additional efforts to monitor its abundance, diet and effects on native fauna, and their responses to mink and/or prey control programs.

In summary, our results stress the importance of considering invasion complexes as integral units (Bull & Courchamp 2009; Zavaleta, Hobbs & Mooney 2001) and evaluating their population dynamics, interactions and impacts on native fauna before introducing control programs aimed at mitigating such impacts – in order to avoid or catering for potential unexpected effects (Courchamp, Chapuis & Pascal 2003) and accommodate multiple, potentially contrasting targets or interests (e.g., single species *vs*. whole ecosystem; Glen *&* Dickman 2005) and not regard as success the protection of a single species.

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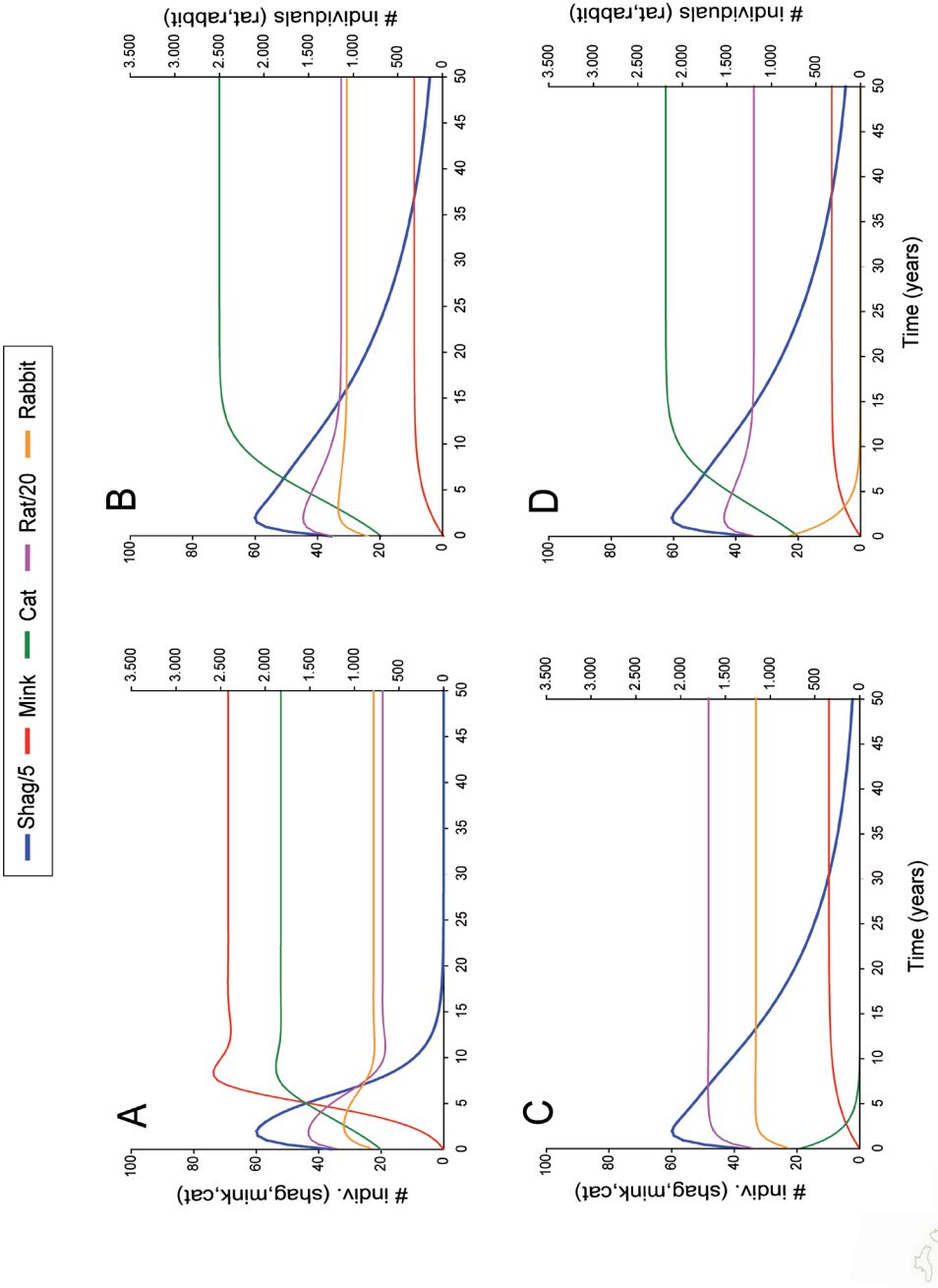
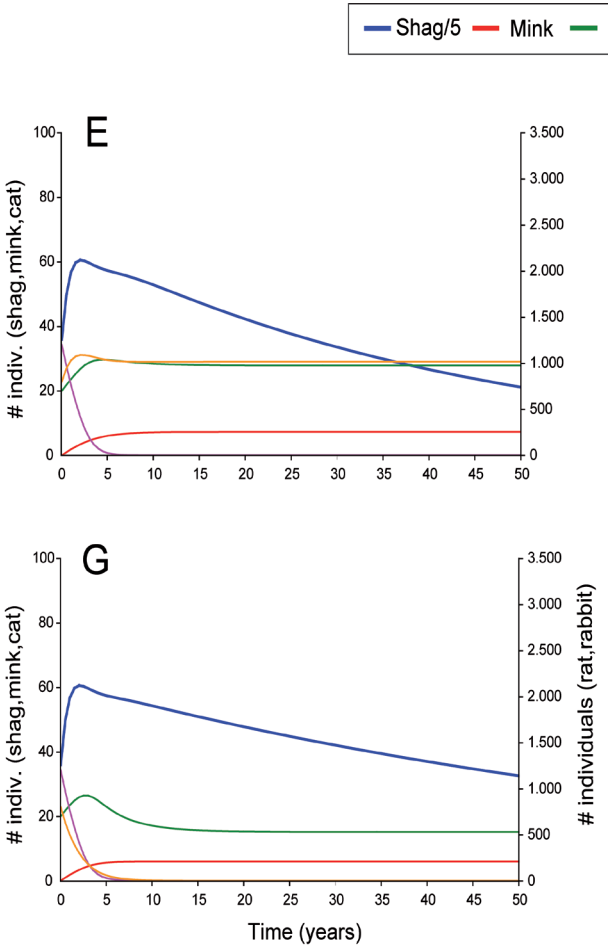
Appendix

Appendix 5.1. Results of different scenarios of the demographic models, corresponding to different control strategies. In all cases, simulations assumed control programs to result in 75% mortality of the target species. A: No control; B: Mink control; C: Mink + cat control; D: Mink + rabbit control; E: Mink + rat control; F: Rabbit + rat control; G: Mink + rabbit + rat control.




Shag/5
Mink
Cat
Rat/20
Rabbit
E
F
G
indiv. (shag,mink,cat)
individuals (rat,rabbit)
Time (years)
0
5
10
15
20
25
30
35
40
45
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20
40
60
80
100
500
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Chapter 6

GENERAL DISCUSSION

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For this thesis, I have studied the invasive process of exotic animals on several protected, continental islands in two different biomes (Mediterranean and Atlantic). In a gradual progression, I increased the complexity of the study systems, assessing integrally the complexity of the relationships between native and invasive species (Chapters 1 and 2) and the invasion complexes (Chapters 3 and 4); including different life cycle phases (Chapter 1), key features of native species (Chapter 2) and multiple interactions between competitors and/or predators and prey (Chapters 3 and 4).

My results confirm the harmful effects invasive animals exert on the native biota of islands. They also emphasize the need for considering different control methods through *ex-ante* studies, examining their effects on both the invasion complex and the native biota, and monitoring their results to detect and correct for unexpected effects. Comprehensive knowledge of the trophic webs established among invasive and native species is critically necessary to achieve these and prevent (or correct for) erroneous or unexpected outcomes of management actions.

Impacts of exotic animals on islands

The effects of invasive mammals can be devastating on islands. My results confirmed this well-known fact, not only for harmful invaders established decades or centuries ago, such as black rats (*Rattus rattus*), European rabbits (*Oryctolagus cuniculus*) and feral cats (*Felis catus*); but also for invasive species that were starting to establish as my study progressed – such as the American mink (*Neovison vison*). American mink exerted even more damaging effects than previously established invaders, directly on individual species or in the form of food-web modulations at community levels. This confirms the results of

previous work in Sálvora and Cíes Islands, which have already documented the consumption of native species, such as seabirds and fish, by mink (Romero 2009, Munilla & Velando 2010). My results suggest that special attention should be paid to this species, in order to prevent the establishment of breeding populations on both islands, supported by the availability of invasive prey (rats and rabbits), which could be particularly damaging for seabird populations of high conservation interest (such as the European shag on Cíes and the lesser black-backed gull on Sálvora).

I also showed that invasive herbivores exert strong effects on island vegetation. First, on Cíes Islands, the recruitment of dune plants was probably strongly reduced by rat granivory (Chapter 4) which is typical of rodents (Heithaus 1981; Brown & Heske 1990; Hulme 1994; Hulme 1997). Second, rats and rabbits consumed the seeds, seedlings and saplings of *Medicago citrina* in Cabrera island (Chapter 2), suggesting that their presence could have caused the absence of this species from the island and its relegation to a couple of small islets, free of rats and rabbit, in the Cabrera Archipelago (Juán 2002; Latorre, Larrinaga & Santamaría 2013). And finally, rabbits browsing in Sálvora Island reduced the growth of *Armeria pubigera* and *Linaria arenaria* (Chapter 3).

Apart from its role as a herbivore and granivore, the rat is an aggressive, opportunistic species. My experiments with artificial nests showed that it is a likely predator of seabird eggs at Sa Dragonera Island, particularly for seabirds with small egg sizes (Chapter 1), confirming the suggestions made by Atkinson (1958) Jones *et al.* (2008).

It is nevertheless when considering the entire invasion complex that synergistic impacts, indirect impacts and complex trophic dynamics are unveiled (Chapters 2, 3 and 4). Synergistic effects arise, for example, on the life cycle of *M. citrina* in Cabrera Island, owing to the impact of rats and rabbits of different

stages of their life-cycle (Chapter 2). More intricate dynamics and indirect effects are observed when considering a whole mammal invasion complex, arising as a consequence of a larger food web within the hosting community (Chapter 3 and 4). In Sálvora, rabbits are a basic resource for the maintenance of the population of minks on the island, which in turn impact severely nesting seagull populations – hence, as Courchamp (2000) posed it, “rabbits may be killing birds” (Chapter.3). Cíes host a larger invasion complex, where both mink and cat prey on both rabbit and rat. Here, control programs could result in or unveil complex trophic cascades, including competitor release (of cat by mink control) and, mesopredator release (following control of mink + cat) or hyperpredation processes (further reduction of mink abundance following mink + rat or mink + rat + rabbit control). My results also confirm a high context-dependence of the effects of biological invasions on islands. For example, rabbits are extremely abundant in Sálvora Island, but do not seem to exert a severe impact on its vegetation; whereas in Cabrera, a much more scarce population would probably constrain the establishment of *Medicago citrina*.

To sum up, even though the particular sensitivity of islands confronting invasions has been recently called into question (Díez *et al.* 2009; Vilà *et al.* 2011), each of these works have confirmed the severe threat that invasive mammals represent for insular biota. Repeated invasion events add new direct and indirect impacts for each new invader and increase the chance of undesired and/or unexpected responses to managing actions. Any new invasion is likely, therefore, to multiply the negative effect of the invasion complex established on an island.

Management actions and the need for pre-control studies

The size of the studied islands ranges from 190 ha (Sálvora) to 1320 ha (Cabrera) and their distance to mainland (Mallorca Island, in the case of Sa Dragonera and Cabrera Islets) range from 0.8 km (Sa Dragonera) to 13.2 km (Cabrera). The mean size of islands where successful eradications have been achieved is 17 ha (Genovesi & Carnevali 2011). This, together with the presence of native biota vulnerable to control methods and the proximity of source populations of the invasive species, seems to prevent reliance on eradication plans on the studied islands (at least, with the current available techniques and funds).

Specific recommendations and/or alternative methods can be deduced from my work, which would be applicable on comparable systems. Rat predation on seabird eggs could be reduced by using deterrent methods based on conditioned taste aversion (LiCl) (Chapter 1). The possibility of combining different methods may also improve success rates; e. g. the use of artificial nests injected with LiCl in Sa Dragonera could be combined with a physical barriers to reduce the access of rats to the colonies. Singular plant species, such as *M. citrina*, could be protected by constraining the access of the most threatening invasive herbivores during the early stages of the life-cycle (Chapter 2). Here again, the possibility of combining different methods, e.g. physical barriers during the early stages of the life-cycle plus herbivore-abundance control during the adult stage, should be explored.

When the species richness of the invasion complexes increases, it becomes increasingly difficult to select adequate management plans. In Sálvora and Cíes Islands, (Chapter 3 and 4), more actions are probably needed aside from the immediate protection of focal native species. Plans that simultaneously consider a variety of possible impacts must be developed for these complex systems,

even when the more urgent and prioritized aim is the safeguarding of a particular species. On Sálvora Island, mink control could suffice to protect seagulls, but it would require permanent maintenance of control efforts - which, over time, would necessarily result in very high costs. Simultaneous control of rabbit abundance may result on more efficient results over the short term and will require only a limited period of control (estimated in 6-10 years), followed perhaps by sporadic control programs (Chapter 3). However, care should be taken to evaluate the effects of invasive herbivore removal on the island's vegetation, which should be measured on previously-defined conservation priorities. On Cíes Islands, in contrast, the situation is more complex, owing to the presence of multiple predators and prey. Controlling mink would slow down the decline of European shag, but the simultaneous control of native prey may be necessary to achieve a significant improvement (Chapter 4). In contrast, the simultaneous reduction of cat and mink may result in mesopredator release effects, which strength would depend on the actual impact of the rat population on shag reproduction. My studies agree with previous work suggesting that management plans focused on single invasive species may be insufficient or even counterproductive (Zavaleta, Hobbs & Mooney 2001; Courchamp, Chapuis & Pascal 2003; Bull & Courchamp 2009), and even the order of removal of single species may be problematic in programs targeting invasion complexes (Collins, Latta & Roemer 2009). Comprehensive pre–control studies are essential not only to assess the severity of the impacts of different invasive species on native biota (and the potential synergies among them), but also to unveil underlying ecological dynamics and identify of the best control strategy. As stated by Vander Zanden (2006), the food-web approach provides "valuable insights into ecological restoration that would not otherwise be attained from a more static, community based approach".

A perfect model that completely covers and defines entire trophic webs may

never be achieved, but the more works on the field, the closer we get towards this ideal. Each new work depicting ecological dynamics of invasion complexes incorporates and tests new processes and their characteristics (Courchamp, Langlais & Sugihara 1999; Roemer *et al.* 2001; Roemer, Donlan & Courchamp 2002). By increasing in fidelity when describing trophic dynamics and their underlying variables (Chapter 3 to 4), the relevance of some of the latter can be assessed under the specific situation of each study system, so that informed decisions about their inclusion in computer models aimed at supporting management decisions can be taken For example, we were not able to demonstrate significant effects of herbivores of native plants (Chapters. 3 and 4) or significant interactions among herbivores (Chapter.3), and decided to exclude these processes from our models. In contrast, diet analysis suggested a strong dependence of invasive predators on invasive prey; hence, these relationships (and the parameters estimated from field data) represented the core of our demographic models (Chapters 3 and 4). Sensitivity analysis of the models may also provide insight into the parameters that are most likely to influence management actions. For example, growth rates of the different species, carrying capacity of one of the prey (rabbit) as well as the predation rates and prey preferences of the predator (mink), had important effects on the output (Chapter 3), similar to suggested in theoretical studies (e.g., Courchamp, Langlais & Sugihara 1999), stressing the importance of improving our parameter estimates using both field studies and data arising from the monitoring of baseline situations and/or management actions.

Summing up to the previous points, the complexity and context-dependency of the dynamic characteristics of invasion complexes stresses the need for case-wise studies of sufficient duration, grounded on sound theory but tested under the specific situation of the systems where the management actions will take place. Furthermore, management actions should customarily include monitoring

programs allowing for *ex-post* evaluation and subsequent refinement (White & Bratton 1980), as well as the detection of undesired or unexpected effects. For practitioners, a robust extracted guideline is perseverance and intensity. Whichever the chosen management plan is, it must be intense and of significant duration. For example, the simulations presented in Chapters 3 and 4 suggest that the most efficient control strategies for Sálvora and Cíes would require a minimal intervention of 8 and 15 years, and a very high efficiency (resulting in >75 % of mortality of the target species).

I would also like to stress the importance of an adequate exchange of information between researchers and practitioners. All of my studies were located in protected areas; two national parks (Atlantic Islands of Galicia National Park and Cabrera Archipelago National Park) and one natural park (Sa Dragonera Natural Park). During my research, the park authorities run control plans for invasive species in all of them: rat control using toxic bait, on Sa Dragonera and Cabrera; trapping of cat and genet, on Cabrera; trapping of mink, on Sálvora; trapping of mink and cat, together with localized, seasonal control of rat on Cíes. Our data and simulations suggest that, although some of the programs represent reasonable solutions to the main conservation programs faced by the park authorities, they are either unlikely to resolve them in the long run or have more cost-effective alternatives (Chapters 3 and 4). On Sálvora and Cíes Islands, simultaneous control of mink and its prey may provide a more suitable strategy for seabird conservation than targeting mink alone. Moreover, in Cíes Islands, predator control (i.e. simultaneous control of mink and cat) may result in increasing rat abundance owing to mesopredator release – with potential consequences on seabird populations (Chapter.4).

The management of invasive species is subsidized with public funds and invasions are one of the issues that require more money from funding agencies

in modern times (Davis 2009). To make this big investment fruitful, the main need is a consensus of local policy makers, practitioners and researchers. Developing a complex and long study depends on the priorities and policies of the (in this case) staff of the protected areas at a lower scale, and at a larger scale, on the environmental priorities of the country, requiring scientific advice (Hulme 2006).

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GENERAL CONCLUSIONS

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- All the invasive mammals addressed in this study exerted negative impacts on the fauna and/or flora of their host islands, at different degrees. Black rat affected native plants by reducing seed survival, as well as seabird communities by preying on their eggs. European rabbit showed an effect on the native plants of two islands, affecting at least two plant species (*Medicago citrina* and *Armeria pubigera*), by reducing the seedling survival of one and the vegetative growth of the other. Diet analysis of feral cat and American mink indicated moderate to strong effects on seabirds, as well as potential effects on other native fauna.

- The increase in the number of invasive species in the study systems resulted in combined, synergic and indirect effects on the native biota. Invasion complexes were associated to intricate ecological dynamics, such as hyperpredation and mesopredator release, with potential consequences on native biota.

- The data and simulations presented here were also used to evaluate the viability of alternative strategies for the control or eradication of the invasive species. For example, the reintroduction of protected plant species on islands can be complemented with specific protection from invasive herbivores, with special emphasis on the protection of the most vulnerable phases of the plant's life cycle. Another example of a potential alternative management strategy outlined in this work is the use of chemical deterrents (conditioned taste aversion) to protect seabird nests from predation by black rat. Species with smaller eggs should be prioritized as their eggs are more vulnerable to predation.

- Studies about invasive species and their impacts are essential for determining the effectiveness of alternative control methods. These studies should be more exhaustive as the complexity of the invasive group increases. The use of simple computer models that incorporate the trophic relationships between invasive and native species proved useful for such purpose. At least one model proved to be particularly sensitive to a number of parameters, such as the growth rates of all species, the

carrying capacity of one of them, as well as the predation rates and prey preferences of the invasive predator. Particular care should therefore be devoted to obtained reliable estimates of these parameters in the field, whether in baseline studies or during the monitoring of the control programs chosen.

- Results exposed in this dissertation suggest that the management of invasion complexes is a demanding undertaking that requires both adequate investments (necessary to ensure high control efficiencies, e.g. >70% mortality in control programs) and prolonged efforts (8 and 10 years in the most optimistic simulation for Sálvora and permanent control on Cíes to prevent seabird colony decline). Such funding rates and durations are much higher than most management plans currently applied in Spain. The application of insufficient, discontinued or sporadic control programs should be avoided, not only because it often represents a waste of money and time, but because it may cause undesired effects (e.g. development of physiological resistance to poison or behavioural avoidance of traps, for invasive species, or increased predation of native biota during transient population peaks of invasive species following the early cessation of control programs).

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CONCLUSIONES GENERALES

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- Todos los mamíferos invasores estudiados ejercieron impactos negativos de distinto grado sobre la fauna y/o flora de las islas que los hospedan. La rata negra afectó tanto a plantas nativas, reduciendo la supervivencia de semillas, como a comunidades de aves marinas, depredando sus huevos. El conejo europeo mostró un efecto sobre plantas nativas en dos islas, afectando al menos a dos especies vegetales (*Medicago citrina* y *Armeria pubigera*), reduciendo la supervivencia de las plántulas de una y el crecimiento vegetativo de la otra. El análisis de la dieta de gato asilvestrado y visón americano indicó efectos de moderados a fuertes sobre aves marinas, además de efectos potenciales sobre otros animales nativos.

- Al aumentar el número de especies invasoras de los sistemas estudiados, aparecieron efectos combinados, sinérgicos e indirectos sobre la biota nativa. Los complejos de invasión están asociados con dinámicas ecológicas complejas como la hiperdepredación y la liberación del mesodepredador, con sus consecuencias potenciales sobre la biota nativa.

- Los datos y simulaciones presentadas fueron utilizados para evaluar la viabilidad de estrategias alternativas al control o erradicación de especies invasoras. Por ejemplo, la reintroducción de especies vegetales protegidas en islas se puede complementar con una protección específica frente a herbívoros invasores; haciendo especial hincapié en las fases del ciclo vital de la planta más vulnerables. Otro ejemplo de posible estrategia alternativa de gestión tratada en el presente trabajo es el uso de aversivos químicos (aversión condicionada al sabor) para proteger los nidos de aves marinas de la depredación por rata negra. Las especies de huevos con menor tamaño deberían tener prioridad ya que sus huevos son más vulnerables a la depredación.

- Los estudios de las especies invasoras y sus impactos son imprescindibles para determinar la efectividad de los métodos alternativos de control. Estos estudios deben ser más exhaustivos cuanto más amplio sea el complejo de invasión a tratar. Se comprobó que el uso de modelos

computacionales simples que incorporan las relaciones tróficas entre especies invasoras y nativas, son altamente útiles para este propósito. Por lo menos uno de los modelos testados reveló ser especialmente sensible a ciertos parámetros, como la tasa de crecimiento de todas las especies implicadas, las tasas de depredación y la preferencia de presas por parte del depredador y la capacidad de carga específica de una de las presas. Se debe prestar especial atención a la recolección de estos parámetros en campo para obtener estimas fiables, tanto para realizar simulaciones como para el monitoreo del plan de manejo finalmente elegido.

- Los resultados expuestos en la presente tesis sugieren que los proyectos de manejo de complejos de invasión son empresas exigentes que requieren tanto inversiones adecuadas (necesarias para asegurar altos niveles de eficiencia en el control, en nuestro caso > 70%) como esfuerzos prolongados (en nuestro caso, de 8 a 10 años en la simulación más optimista para Sálvora, y control permanente en las Cíes para prevenir el declive de las colonias de aves marinas). Tales niveles de financiación y duración son mucho más de lo que hoy en día se aplica en España. La ejecución de programas de control insuficientes, discontinuos o esporádicos se deben evitar, no solo por la pérdida de tiempo y dinero que supone, sino porque puede llevar a efectos no deseados, como el desarrollo de resistencia fisiológica a venenos o la evasión aprendida de trampas en el caso de las especies invasoras, o incluso tasas de depredación inusualmente altas de biota nativa, durante picos poblacionales de especies invasoras tras el cese temprano de programas de control.

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